Tree Species Diversity and the Functioning and Stability of a Managed Forest in Central Europe

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

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Zürich 2014

I dedicate this thesis to the many people I love

"Life is not about waiting for the storm to pass,

It is about learning to dance with the rain."

(Vivian Greene)

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Acknowledgements

I first would like to thank Andy Hector for his supervision and support over the past four years. Thank you for believing in me and allowing me freedom in my work, and thank you for always knowing when I needed inputs, time, or a bit of pressure. It has been an honour to collaborate with you, and a great opportunity to broaden my views on ecology.

I would also like to thank my co-supervisors Lindsay Turnbull, David Frank, and Tim Paine for their guidance and help. A special thanks to Tim who spent countless hours helping me with study design, fieldwork, graphics and analysis, sometimes late at night with a beer!

Many thanks to Radim Matula, Martin Svatek, Daniel Volarik, Tomas Zid, and all my collaborators from the Czech Republic. None of this would have been possible without this incredibly fruitful collaboration. Thank you for your hard work on the field, thank you for building ideas and projects together, and for having me so many times in Brno and always making me feel so welcome. I am sure that this collaboration will be a long lasting one, because it is built on scientific interest, mutual respect, and friendship.

Thank you to all my colleagues at the university of Zürich for sharing such a nice time these past years. Especially, thank you Maja Weilenmann for your help, love and support. I cannot start to explain how

meeting you changed my life in Zürich, not to even mention all of your help with the administration. Thank you also to Isabel Schöchli without whom this institute would collapse. Your efficiency at work and your kindness are legendary! Thanks Janina and Gabriela for the german translation. And special thanks to Chris Philipson for your comments and ideas on my manuscripts, and all your emotional support during these last few months. I could not have stayed peaceful without you here.

Thanks to all the people who have influenced and guided my scientific path, especially Christophe Thébaud who always finds time to give me advice when I need it. You've always been a mentor to me.

Finally, a big thanks to all of my friends and family, here and abroad, for their love, trust, time, energy, support. A special thank to Claire, my adopted sister and beloved flat mate who makes life here so sweet. Thanks for the many parties, dinners, discussions, laughs, cries, and simply for all the little things of everyday life… I still don't know how I will manage to live on my own after all these years sharing a flat with you! Thanks to my parents Régis and Laurence, my sister Louise, my godfather Patrick and all my friends from France for being such an important part in my life despite the distance. Merci pour votre amour infini, vous savez toujours me guider dans mes choix au moment propice. And thanks to the family I chose here, especially Sarah, Oliver, Janina, and Nico, but also Dzaeman, Enrica, Martin, Philippe, Adele, Katie and all the others, the list would be too long. It still amazes me how magical these friendships are, and how much trust, love, and understanding there is between all of us. You're a precious gift.

Summary

Forests cover a third of the earth's land area, host most of the terrestrial diversity, and provide us with services that are essential for our survival and well-being. Sadly forests, like most ecosystems, are threatened by climate change, biodiversity loss, pollution and land use change. In Europe, most forests are managed for timber, and their diversity is at least partially manipulated. There is increasing evidence that biodiversity enhances ecosystem functioning and stability, and is therefore likely to sustain the services we are interested in. Forests however, are challenging systems to investigate, because trees are tall and long-lived organisms that require studies extending in space and time. In this thesis, I examine the effects of tree species diversity on several aspects of the functioning and stability of a managed forest in the Czech Republic.

In **Chapter 1**, I use trees' annual rings to estimate their age, and explore the historical management of this central European forest. I find that younger trees were found in more diverse stands, indicating that shifts in forest practices over the past century have increased species diversity. Using spatial mapping technology, I assess the amount of wood extracted per unit of time and area at every stand. I find that it was unaffected by species diversity, and rather correlated to the abundance of *Picea abies* (Norway spruce) and *Fagus sylvatica* (European beech), the most economically important species in the region. Our study suggests that forestry has evolved to answer societal demands for more naturalistic forest management, even if the higher diversity doesn't show any positive or negative effect on wood extraction.

In **Chapter 2**, I use tree ring width as a record of past growth to evaluate the growth rate of individual trees, as well as the temporal variation in individual growth. I find that growth rates are species and age specific, and increase by 18 to 28% when species diversity increases from one to four species. The temporal variation in individual growth rates, namely the coefficient of variation, is also species specific. It decreases with increasing density, but is unaffected by species diversity. My results suggest that species diversity directly affects the growth of individual trees in this managed forest, independently of density, and in the same way for all species. They also reveal that diversity might not be such a strong driver for stability at the individual tree level. I highlight that more theory and experiments are needed to understand the processes by which diversity and competition affect the stability of ecosystems, and especially the stability of the individual organisms that compose them.

In **Chapter 3**, I use classical dendrochronological methods to look at the climatic forcing in tree ring time series. I find that in this water-limited forest of central Europe, trees are mostly limited by drought in the current growing season. These responses to climate are however very species specific, and some species like *Quercus petraea* (Sessile oak) are much more drought tolerant than others. I also find that the sensitivity of growth to climate is unaffected by the surrounding diversity, suggesting that these responses to climate are very consistent within species. However more work is needed to understand how these species-specific responses to climate act on asynchrony between species, and therefore participate in ecosystem level stability.

In **Chapter 4**, I analyze the effects of tree diversity on the species richness of different groups of understory organisms, namely herbs, earthworms and beetles. I use structural equation models to disentangle

the direct effects of tree species diversity and identity on the understory, from those mediated by changes in abiotic features such as light availability, litter thickness or soil chemical properties. I find that tree diversity directly promotes the diversity of earthworms and saproxylic beetles, which are two important groups of litter-dwelling decomposers. Contrary to previous work, I find a negative effect of tree diversity on herb diversity, mediated by a greater canopy cover. This explicitly shows that trees and herbs compete for light, and that trees outcompete herbs. Tree species identity also has various effects on understory groups, implying that some monocultures might be advantageous and therefore worth sustaining. These results emphasize the need for more modeling efforts to integrate the direct and indirect effects of species diversity and identity on different ecosystem functions, if we are to inform forest practices in the face of accelerating climate change.

Zusammenfassung

Wälder bedecken ein Drittel der Erdoberfläche, beherbergen einen Grossteil terrestrischer Diversität und versorgen uns mit Gütern, die für unser Leben und Wohlergehen essentiell sind. Umso bedauerlicher ist es, dass Wälder, wie die meisten Ökosysteme, stark durch Klimawandel, Biodiversitätsverlust, Umweltverschmutzung und Landnutzungsveränderungen gefährdet sind. In Europa werden die meisten Wälder zur Holzproduktion bewirtschaftet und ihre Diversität zumindest teilweise beeinflusst. Gleichzeitig mehren sich die Indizien, dass Biodiversität zur Funktions- und Stabilitätserhaltung von Ökosystemen beiträgt, und somit verantwortlich ist für die Erhaltung der Ökosystem-Dienstleistungen, die für uns von Interesse sind. Das Erforschen von Wäldern ist jedoch eine Herausforderung, da Bäume grosse und langlebige Organismen sind, die zeitlich und räumlich ausgedehnter Studien bedürfen. In dieser Arbeit untersuche ich die Effekte der Baumartenvielfalt auf diverse Aspekte der Funktion und Stabilität bewirtschafteter Wälder in Tschechien.

In **Kapitel 1** schätze ich anhand von Jahrringen das Alter der Bäume und untersuche die historische Bewirtschaftung dieses zentraleuropäischen Waldes. Ich konnte herausfinden, dass jüngere Bäume in artenreicheren Beständen vorkommen, was andeutet, dass Veränderungen der Bewirtschaftungspraktiken im letzten Jahrhundert zu einem Anstieg der Artenvielfalt geführt haben. Mithilfe räumlicher Kartierungstechnologien konnten Daten über die extrahierte Holzmenge pro Zeit- und Flächeneinheit für jeden Bestand erhoben werden. Diese war, wie sich zeigte, nicht abhängig von der Artenvielfalt, sondern von

dem Vorkommen der wirtschaftlich wichtigsten Arten der Region, *Picea abies* (Norwegische Fichte) und *Fagus sylvatica (Europäische Buche).* Diese Studie suggeriert, dass die Forstwirtschaft sich entwickelt hat um der gesellschaftlichen Nachfrage nach natürlicher Bewirtschaftung entgegenzukommen, auch wenn keine positiven oder negativen Effekte der erhöhten Biodiversität auf die Holzextraktion nachweisbar sind.

In **Kapitel 2** nutze ich die Jahrringbreite zur Beurteilung von Wachstumsraten einzelner Individuen als auch derer temporären Variation. Ich habe herausgefunden, dass die Wachstumsraten art- und altersspezifisch sind und um 18-28% ansteigen, wenn die Artenvielfalt von einer zu vier Arten ansteigt. Die temporäre Variation individueller Wachstumsraten, d.h. der Variationskoeffizient, ist ebenfalls artspezifisch. Der Variationskoeffizient nimmt ab mit steigender Dichte, ist jedoch nicht abhängig von der Artenvielfalt. Meine Ergebnisse weisen darauf hin, dass die Artenvielfalt einen direkten Einfluss auf das Wachstum individueller Bäume in diesem bewirtschafteten Forst hat, unabhängig von der Dichte und gleichermassen für alle Arten. Sie zeigen auch, dass Diversität ein möglicherweise nicht so starker Einflussfaktor für die Stabilität auf der Ebene des einzelnen Individuums ist. Ich möchte betonen, dass weitere theoretische Arbeit sowie Experimente vonnöten sind um die Prozesse zu verstehen, mit denen Diversität und Konkurrenz die Stabilität von Ökosystemen und insbesondere die Stabilität der einzelnen Individuen, aus denen diese bestehen, beeinflussen.

In **Kapitel 3** nutze ich klassische dendrochronologische Methoden um klimatische Einflüsse in Jahrringfolgen zu untersuchen. Ich konnte herausfinden, dass im untersuchten wasserlimitierten Forst in Zentral-Europa Bäume überwiegend durch Trockenheit der aktuellen Wachstumsperiode limitiert sind. Diese Reaktionen auf das Klima sind

jedoch deutlich artspezifisch und manche Arten wie *Quercus petraea* (Traubeneiche) sind toleranter gegenüber Trockenheit als andere. Ich konnte ausserdem herausfinden, dass die Sensitivität des Wachstums gegenüber klimatischen Bedingungen unabhängig ist von der Diversität der Umgebung, was suggeriert, dass Reaktionen auf das Klima innerhalb einer Art gleichbleibend sind. Weitere Studien sind notwendigum zu verstehen, wie diese artspezifischen Reaktionen auf das Klima auf die Asynchronie zwischen den Arten wirken und somit zur Stabilität auf Ökosystem-Ebene beitragen.

In **Kapitel 4** analysiere ich die Effekte der Artenvielfalt der Bäume auf den Artenreichtum verschiedener Gruppen von Organismen des Unterholzes, im speziellen von Kräutern, Regenwürmern und Käfern. Ich nutze strukturelle Gleichungsmodelle zur Trennung direkter Effekte der Baumartenvielfalt und -identität auf das Unterholz, von Effekten, die durch Veränderungen abiotischer Bedingungen wie Lichtzufuhr, Laubdichte oder bodenchemischer Faktoren hervorgerufen wurden. Ich konnte herausfinden, dass die Baumartenvielfalt die Artenvielfalt von Regenwürmern und saprophytischen Käfern, welche zur Gruppe wichtiger Destruenten zählen, direkt begünstigt. Ich konnte im Gegensatz zu vorhergehenden Arbeiten einen negativen Effekt der Baumartenvielfalt auf die Kräuterdiversität feststellen, hervorgerufen durch einen erhöhten Deckungsgrad der Baumschicht. Dies zeigt eindeutig, dass Bäume und Kräuter um Licht konkurrieren, und dass Bäume den Kräutern in diesem Konkurrenzkampf überlegen sind. Ausserdem hat die Artidentität der Bäume verschiedene Auswirkungen auf die im Unterholz lebenden Organismengruppen, womit manche Monokulturen von Vorteil sein könnten und erhalten werden sollten. Diese Ergebnisse machen den Bedarf nach Modelansätzen zur Integration von direkten und indirekten Effekten der Artenvielfalt und -identität auf verschiedene Funktionen des

Ökosystems deutlich, wenn wir forstwirtschaftliche Methoden angesichts des fortschreitenden Klimawandels verbessern wollen.

Résumé

Les forêts couvrent un tiers de la surface des terres émergées, accueillent la plupart des espèces et sont garantes de la biodiversité terrestre. Elles fournissent des services qui sont essentiels à notre survie et à notre bien-être. Malheureusement les forêts, comme presque tous les écosystèmes, sont menacées par les changements climatiques, la réduction de la biodiversité, la pollution et l'aménagement des territoires. En Europe, la majorité des forêts sont gérées pour leur bois, et leur diversité est au moins partiellement manipulée. Des études en nombre croissant montrent que la biodiversité améliore le fonctionnement et la stabilité des écosystèmes, et est donc susceptible de maintenir les services qui nous intéressent. Les forêts sont cependant des systèmes difficiles à étudier, parce que les arbres sont des organismes de grande taille, à longue espérance de vie. Les études doivent donc s'étendre dans le temps et l'espace. Dans cette thèse, j'examine les effets de la biodiversité des arbres sur plusieurs aspects du fonctionnement et de la stabilité d'une forêt gérée de la République tchèque.

Dans le **Chapitre 1**, j'ai utilisé les cernes de croissance des arbres pour estimer leur âge et explorer les changements à travers l'histoire de la gestion de cette forêt d'Europe centrale. J'ai découvert que les jeunes arbres étaient situés dans les parcelles les plus diverses, indiquant que des changements dans les pratiques forestières ont augmenté la biodiversité au cours du siècle dernier. Grâce à des méthodes cartographiques, j'ai évalué la quantité de bois extrait par unité de temps et de surface dans chaque parcelle. Je n'ai détecté aucun effet dû à la biodiversité, mais par contre j'ai trouvé que l'extraction de bois était corrélée à l'abondance de

Picea abies (Epicéa commun) et de *Fagus sylvatica* (Hêtre commun), les deux espèces les plus importantes dans la région sur le plan économique. Cette étude suggère que la foresterie a évolué suite aux demandes sociétales pour que les forêts gérées se rapprochent des forêts naturelles en intégrant plus d'espèces, même si cette biodiversité n'a montré aucun effet (ni positif ni négatif) sur l'extraction de bois.

Dans le **Chapitre 2**, j'ai utilisé la largeur des cernes de croissance pour estimer le taux de croissance des arbres, ainsi que la variation temporelle de leur taux de croissance, appelée coefficient de variation. J'ai trouvé que le taux de croissance des arbres était spécifique à l'espèce et à l'âge, et montrait une augmentation de 18 à 28% quand la biodiversité passe de une à quatre espèces. Le coefficient de variation était également spécifique à l'espèce et diminuait quand la densité d'arbres augmentait, mais qu'il n'était pas affecté par la biodiversité. Mes résultats suggèrent que dans cette forêt aménagée, la biodiversité affecte directement la croissance individuelle des arbres, indépendamment de la densité, et de la même manière pour toutes les espèces. Ils révèlent aussi que la diversité n'aurait pas d'influence sur la stabilité temporelle, au moins au niveau de l'individu. Je souligne que plus de théorie et d'expériences sont nécessaires pour comprendre les processus par lesquels la diversité et la compétition affectent la stabilité des écosystèmes, et en particulier la stabilité des organismes individuels qui les composent.

Dans le **Chapitre 3**, j'ai utilisé des méthodes dendrochronologiques classiques pour étudier l'impact des variations climatiques sur les séries temporelles obtenues à partir des cernes de croissance. J'ai confirmé que dans cette forêt d'Europe centrale où l'eau est le facteur limitant, la croissance des arbres est essentiellement limitée par la sécheresse éventuelle au cours de la saison de croissance. Cette réponse au climat est

de plus spécifique à chaque espèce d'arbre. Certaines espèces comme *Quercus petraea* (Chêne sessile) sont ainsi beaucoup plus tolérantes à la sécheresse que d'autres. J'ai aussi constaté que la sensibilité de la croissance au climat n'était pas affectée par la diversité environnante, ce qui suggère que ces réponses au climat sont très cohérentes au sein de chaque espèce. Cependant plus de travail est nécessaire pour comprendre comment ces réponses spécifiques aux espèces agissent sur l'asynchronie entre espèces, et participent à la stabilité du niveau de l'écosystème.

Dans le **Chapitre 4**, j'ai analysé les effets de la diversité des arbres sur la richesse en espèces de différents groupes d'organismes du sous-bois : herbes, vers de terre et coléoptères. J'ai utilisé des modèles d'équations structurelles pour distinguer les effets directs de la diversité et de l'identité des espèces d'arbres sur le sous-bois, de ceux, indirects, véhiculés par des changements abiotiques tels que la disponibilité en lumière, l'épaisseur de la litière, ou les propriétés chimiques du sol. J'ai découvert que la diversité des arbres favorisait directement la diversité des vers de terre et des coléoptères saproxyliques, qui sont deux groupes importants de décomposeurs vivant dans la litière. Contrairement aux travaux précédents, j'ai détecté un effet négatif de la diversité des arbres sur la diversité des herbes, véhiculé par un couvert arboré plus important. Cela montre explicitement que les arbres et les herbes sont en compétition pour la lumière, et que les arbres l'emportent sur les herbes. L'identité des espèces d'arbres ayant également des effets différents sur les groupes sous-bois, certaines monocultures peuvent être avantageuses et donc valent la peine d'être maintenues. Ces résultats soulignent la nécessité de fournir plus d'efforts pour modéliser les effets directs et indirects de la diversité et de l'identité des espèces d'arbres sur les différentes fonctions des écosystèmes, afin d'informer les pratiques forestières face à l'accélération des changements climatiques.

General Introduction

On the importance of forests

Forests cover 30% of the earth's land area, are home to 80% of our terrestrial biodiversity, and trade in forest products is estimated at more than 300 billion dollars per year (FAO 2010). They provide humanity with essential services that are cultural, economical (food, medicine, fuel, fibers…), and ecological (biogeochemical cycling, water and air filtering, decomposition…) ("Millennium Ecosystem Assessment" 2005; Naeem *et al.* 2009). Sadly forests, like most ecosystems, are threatened by anthropogenically-induced climate change, air and water pollution, land use, and biodiversity loss (Rockström *et al.* 2009; Rands *et al.* 2010; Hooper *et al.* 2012). Trees are tall and long-lived organisms, making forests complex ecosystems that vary greatly in space and time, and this complexity requires adapted study design (Nadrowski *et al.* 2010).

Managed forests in Europe

In Europe (excluding Russia), forests cover more than 200 million hectares, 97% of which are managed by humans (FAO 2010; FOREST EUROPE *et al.* 2011). In 2008, the forest sector (including the manufacturing of wood and paper products) contributed to 1% of the gross domestic product (FOREST EUROPE *et al.* 2011), and 30% of the forest area is designated for wood production (FAO 2010). Whether species diversity favors production has been a continuous debate, but the increasing societal demands for sustainable and naturalistic forestry is pushing towards more diverse forests (Spiecker 2003). Today still, only 20% of the forested European area is covered with more than three species, and 5% with more than six (FOREST EUROPE *et al.* 2011). In a

context of biodiversity loss, it is important to understand how biodiversity affects the functioning and stability of forests, in order to inform management practices and insure a sustainable provision of forest services.

Biodiversity and ecosystem functioning (BEF) in forests

The recent and increasing loss of biodiversity has motivated ecologists to understand the relationship between biodiversity and ecosystem functioning (Cardinale *et al.* 2011; Hooper *et al.* 2012). Most of the evidence comes from fast growing systems like grasslands, where the positive but saturating relationships generally observed indicate that the initial loss of a single species might not have such a strong effect on ecosystem function, but this effect is non-linear and accelerates with the loss of additional species (Hooper *et al.* 2005). Besides, a greater number of species is required to sustain several ecosystem functions simultaneously (Hector & Bagchi 2007; Zavaleta *et al.* 2010; Gamfeldt *et al.* 2013).

Because of their complexity, forests have been much less investigated, and wood production is often the only function considered (Nadrowski *et al.* 2010; Cardinale *et al.* 2011). The positive effect of biodiversity on wood production can be due to enhanced individual tree growth (Potvin & Gotelli 2008; Vilà *et al.* 2013) or increased tree density (Barrufol *et al.* 2013). Forest diversity has also been found to have positive or at least neutral effects on other functions (Nadrowski *et al.* 2010) such as decomposition (Madritch & Cardinale 2007; Scherer-Lorenzen *et al.* 2007a), fine root production (Lei *et al.* 2012), or the diversity of soil invertebrates (Sobek *et al.* 2009). Some planted experiments have been designed to explore the simultaneous effects of diversity on different

forest functions (Scherer-Lorenzen *et al.* 2007b; Hector *et al.* 2011), but these experiments are still young, and not always suited to understand how mature but managed forests function.

Biodiversity and ecosystem stability (BES) in forests

Another important aspect of ecosystem functioning is its sustainability under rapidly changing conditions. Over the past decade, a growing body of research has focused on how species diversity affects the temporal variation in grassland productivity (Hector *et al.* 2010; de Mazancourt *et al.* 2013; Loreau & de Mazancourt 2013). Most studies found population-level productivity to be more variable through time as species diversity increases, as a result of increased number of interspecific interactions (Hector *et al.* 2010; Roscher *et al.* 2011; Cadotte, Dinnage & Tilman 2012). Ecosystem-level productivity on the other hand, is stabilized by species diversity, partly because of the asynchrony of different species in a fluctuating environment (Gonzalez & Loreau 2009; Loreau & de Mazancourt 2013).

Evidence on the effects of diversity on forest stability is scarce, despite the urge to maintain forest services in the face of global change (Thompson *et al.* 2009). Tree species differ in their demography, physiology, and phenology, all of which affect their response and sensitivity to climatic conditions (Babst *et al.* 2013). To our knowledge, only a recent study explored growth compensations between species following a disturbance in mixed forests (Perot, Vallet & Archaux 2013). Yet, there is a huge potential to learn more about ecosystem stability, resistance and resilience in forests, especially because contrary to clonal grasses, it is possible to look at the effects of diversity on the temporal stability of individual trees.

In this thesis, I therefore design a study focused on individual trees, in a managed forest of central Europe, where sites of increasing diversity are sampled. Using tree rings as a record of plant growth, I investigate the effects of diversity and other forest properties on individual trees. Contrary to planted experiments, this method allows exploring the past growth of adult trees, without having to wait decades for seedlings to grow.

The Training Forest Enterprise

The Training Forest Enterprise (TFE) is located in the Czech Republic in central Europe (Fig. 1). This experimental has been owned and managed by the Mendel University in Brno since 1923, and today it is used for both practical training in forestry as well as commercial endeavors (Truhlář 1997). It is more than 10 thousand hectares, and composed of 4000 forest stands, for which topography, bedrock, and soil type are known (www.mapserver-slp.mendelu.cz/). Every ten years, the volumetric composition, forest type, age and density are estimated. Today, the forest is composed of 54% of coniferous and 46% of coniferous species, in stands of various forest types and levels of species diversity, making it an adequate place to study the effects of diversity on forest functioning and stability.

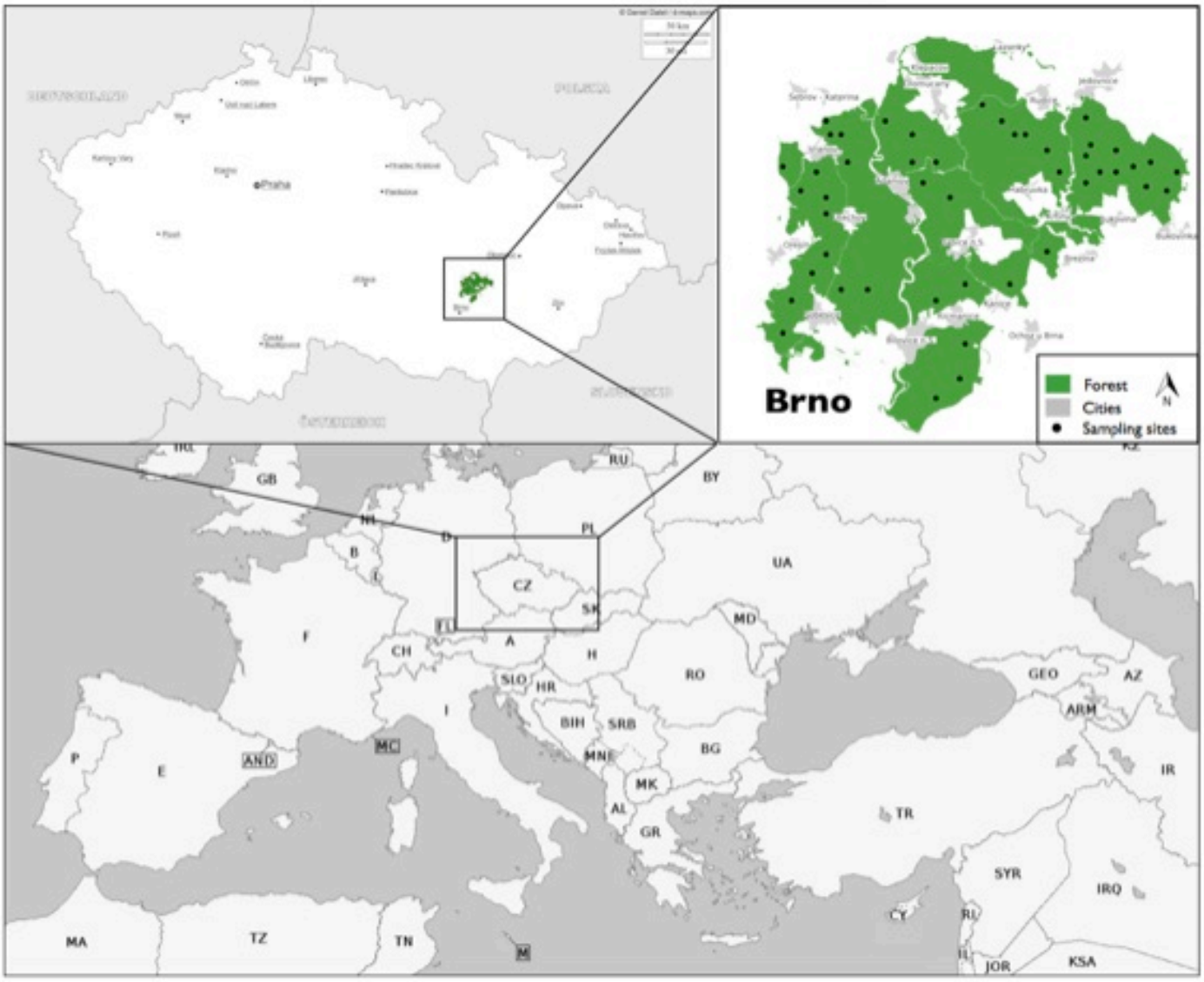

Figure 1: The study location. The Training Forest Enterprise is located north of Brno, in the Czech Republic, in central Europe.

Site	Tree Composition*	Tree Focal SR**	Tree Observed SR**	Tree Focal eH'**	Tree Observed eH'**	Tree Total Density (BA/ha)	Herb SR	Earthworms SR	Beetles SR	Area (ha)	X (UTM)	Y (UTM)	Altitude (m)	Slope (%) ***	Aspect ***	Soil type	pH	C/N ratio	P	Humus (g)	Canopy cover
1	F	1	4	1.28	1.28	231	14	0	7	0.12	627353	5464546	528	0.54	0.99	cambisol	4.4	14.0	3.0	185	0.91
2	F	1	3	1.85	1.95	145	32	1	8	0.17	625338	5465117	525	12.25	0.55	cambisol	5.2	17.9	4.0	171	0.93
3	F	1	3	1.08	1.08	205	27	2	10	0.13	626477	5460544	499	8.75	1.00	leptosol	5.3	18.3	13.0	138	0.93
4	L	1	1	1.00	1.00	253	42	1	6	0.08	623002	5464566	476	4.01	0.89	cambisol	4.2	33.2	7.5	169	0.68
5	L	1	5	1.49	1.88	320	34	NA	6	0.07	623778	5458754	395	2.81	0.95	cambisol	5.1	26.8	4.0	139	0.81
6	L	1	4	1.15	1.15	217	33	2	8	0.08	618045	5459084	402	9.08	0.94	cambisol	5.0	27.7	3.5	199	0.54
7	P	1	3	1.06	1.06	426	25	3	8	0.17	628034	5464376	561	5.86	0.48	cambisol	3.9	14.6	3.0	242	0.85
8	P	1	2	1.11	1.11	229	35	2	10	0.16	628718	5464472	579	16.04	0.03	cambisol	3.9	21.5	7.5	124	0.54
9	P	1	3	1.18	1.29	384	22	1	16	0.18	628269	5464456	568	2.73	0.97	luvisol	4.0	17.5	3.5	261	0.72
10	Q	1	2	1.27	1.27	194	37	4	6	0.15	618130	5457799	409	2.89	1.00	cambisol	4.4	23.3	4.0	76	0.71
11	Q	1	1	1.00	1.00	297	33	2	7	0.10	616922	5458532	353	4.30	0.86	cambisol	4.9	18.3	5.5	80	0.65
12	Q	1	1	1.00	1.00	223	37	3	8	0.09	616907	5455897	325	4.44	0.82	cambisol	6.2	22.3	5.5	57	0.67
13	FL	2	3	2.41	2.41	269	22	0	8	0.26	623199	5465278	469	11.53	0.74	leptosol	4.6	28.6	2.0	121	0.88
14	FL	2	3	2.09	2.09	307	1	2	7	0.16	625089	5464692	545	6.20	1.00	cambisol	3.9	23.5	4.5	183	0.90
15	FL	2	6	2.52	2.67	350	10	3	15	0.25	623858	5463521	459	6.58	0.09	leptosol	4.2	24.7	4.5	187	0.94
16	FP	2	4	2.27	2.34	216	33	2	8	0.33	627422	5463401	510	4.78	0.69	cambisol	4.3	13.4	2.5	201	0.86
17	FP	2	5	2.20	2.32	248	21	3	4	0.28	617897	5463904	476	8.22	0.23	cambisol	4.3	13.4	3.0	184	0.91
18	FP	2	7	2.46	2.78	298	24	3	13	0.28	626666	5463143	474	13.48	0.91	cambisol	4.2	11.0	2.5	229	0.87
19	FQ	2	2	1.97	1.97	161	12	1	10	0.22	620479	5462949	365	8.54	0.96	cambisol	4.7	32.8	4.0	100	0.86
20	FQ	2	4	2.00	2.00	123	48	NA	11	0.20	621361	5462172	419	6.59	0.92	cambisol	5.1	19.5	3.5	89	0.88
21	FQ	2	2	1.80	1.80	197	27	1	5	0.29	619395	5457532	385	19.63	0.71	cambisol	5.1	30.0	3.5	122	0.87
22	LP	2	3	1.78	1.78	377	17	2	10	0.24	629921	5463645	563	12.37	0.60	cambisol	4.2	20.1	3.5	236	0.78
23	LP	2	7	2.51	3.47	293	24	2	9	0.19	617355	5464287	451	17.19	0.45	cambisol	4.6	28.5	3.5	145	0.61
24	LP	2	4	2.26	2.26	322	31	3	10	0.28	627356	5463118	517	4.06	0.17	cambisol	4.3	23.7	6.5	165	0.73
25	LQ	2	3	2.06	2.06	260	39	3	10	0.29	619018	5457435	440	3.40	0.99	cambisol	5.7	19.6	11.0	130	0.62
26	LQ	2	3	1.67	1.67	251	39	NA	11	0.21	622833	5454330	421	1.71	0.18	cambisol	5.1	25.1	4.5	107	0.93
27	LQ	2	4	2.16	2.35	262	23	1	4	0.19	617107	5461504	440	9.99	0.94	cambisol	4.9	17.9	3.5	98	0.69
28	PQ	2	4	2.75	2.75	257	27	3	12	0.17	628453	5462933	560	7.46	1.00	cambisol	4.3	15.8	6.5	148	0.81
29	PQ	2	5	3.06	3.06	280	31	2	10	0.10	619177	5460883	459	0.10	0.99	luvisol	4.1	22.4	5.0	141	0.88
30	PQ	2	5	2.11	2.73	301	30	4	5	0.19	623034	5455587	313	15.59	0.05	cambisol	5.1	20.9	3.0	106	0.84
31	FLP	3	6	3.05	3.10	264	17	2	6	0.31	630568	5462769	545	0.78	0.47	cambisol	4.0	24.1	6.0	222	0.93
32	FLP	3	4	2.73	2.73	268	25	2	7	0.30	625123	5464073	533	1.88	0.44	leptosol	4.4	20.7	4.5	164	0.87
33	FLP	3	5	2.85	3.19	267	24	3	5	0.31	617648	5462407	509	4.58	0.82	cambisol	4.5	31.4	10.0	186	0.77
34	FLQ	3	6	2.97	3.37	148	20	NA	10	0.34	622775	5457895	356	8.79	0.99	cambisol	5.5	31.9	4.5	150	0.96
35	FLQ	3	6	2.99	3.04	236	16	4	6	0.38	619051	5457556	428	5.81	0.29	cambisol	5.8	19.9	6.0	123	0.90
36	FLQ	3	6	3.19	3.25	286	8	4	13	0.28	624565	5463529	517	7.78	0.89	leptosol	5.4	19.3	3.5	187	0.90
37	FPQ	3	4	3.07	3.07	246	19	2	13	0.24	629682	5463212	546	6.57	0.99	cambisol	4.0	21.3	9.5	169	0.88
38	FPQ	3	6	3.03	3.11	235	47	4	9	0.26	617153	5462448	450	14.92	0.50	cambisol	5.1	24.7	3.0	142	0.88
39	FPQ	3	6	3.09	3.29	178	23	3	14	0.42	628489	5463530	576	0.35	0.69	cambisol	4.5	19.5	6.0	128	0.91
40	LPQ	3	5	2.76	3.50	257	48	4	11	0.25	618606	5457507	393	6.56	0.88	cambisol	4.6	22.8	7.5	127	0.73
41	LPQ	3	5	2.93	3.30	186	50	1	4	0.40	617978	5459377	406	7.57	1.00	luvisol	4.8	37.7	2.5	146	0.54
42	LPQ	3	5	3.25	3.88	338	33	3	8	0.28	617034	5461338	429	11.40	0.83	cambisol	5.2	17.6	4.5	131	0.78
43	FLPQ	4	6	3.93	3.99	200	25	4	10	0.44	615884	5462673	460	2.97	0.93	cambisol	4.6	20.6	5.0	115	0.83
44	FLPQ	4	7	3.82	4.34	173	13	3	9	0.45	628036	5462960	537	3.27	0.53	cambisol	4.7	14.0	4.5	131	0.92
45	FLPQ	4	7	2.78	3.23	292	8	2	3	0.59	621223	5464653	474	1.40	0.01	cambisol	4.3	34.0	2.0	213	0.91

Table 1: Information on biotic and abiotic features of the sampling sites.
*The letters designate the initials of each species.
**Focal diversity was calculated for study species only, and observed diversity for all canopy species. SR: Species richness, eH': effective Species Richness.
***Slope and Aspect are calculated from the (x,y,z) coordinates of the trees. The aspect is a value comprised between 0 (full north) and 1 (full south).

Sampling design

Four of the five most abundant and economically important species were included in this study: and evergreen conifer, Norway spruce (*Picea abies*), a deciduous conifer, European larch (*Larix decidua*), and two deciduous broadleaved species Sessile oak (*Quercus petraea*), and European beech (*Fagus sylvatica*). Sites dominated by all combinations of these focal species were sampled, and replicated three times each. Our sampling design thus incorporated 45 forest sites and 15 different species compositions (Table 1). Every site was mapped with the Field-Map technology (Hédl *et al.* 2009, http://www.fieldmap.cz/), a software and hardware combining a measuring rangefinder with an electronic compass, and aimed at real time mapping of forests. For every tree mapped, its spatial position (x-,y-, and z-coordinates) was measured, a species was assigned, the DBH was measured, and its health status (dead or alive) was recorded. From these maps we could assess the exact species diversity, tree density, and by estimating the age of every stump, we could determine the amount of wood extracted in the last few years. We selected a few target trees of each species that we cored, and for which we counted and measured annual rings. These tree ring width time series were used to identify tree age, growth, and response to climate. Finally, we established transects at each site on which we collected beetles, earthworms and censused herb diversity and abundance. On each transect, we also measured canopy cover, humus mass and some soil properties.

Conclusions

In this thesis, I examine the effects of tree species diversity on different ecosystem properties. I use tree rings to explore the effects of diversity on individual tree growth and temporal variation. Using dendrochronological methods, I study the response of each species to climatic drivers. And finally, I look at the direct and indirect effects of tree

species identity and diversity on the diversity of understory organisms that are important for decomposition and nutrient cycling. I discuss the effects of species diversity on multifunctionality and open possibilities for further work on forest stability.

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Chapter 1

Managing for diversity: Evidence for changing practices in a central European forest.

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Abstract

Forests are one of the most important ecosystems on Earth as they provide humanity with vital services, including wood production for timber and carbon sequestration. Overall forest productivity can be increased by tree diversity, because of complementarity between species. Forest management, by directly manipulating species diversity, affects the functioning of these forests, especially in Europe where little primary forest cover remains. To determine the effects of applied forestry practices on diversity and productivity, we studied the Mendel University's experimental forest in the Czech Republic. Younger trees were found in sites of higher species richness and lower size diversity, indicating that shifts in management practices over the last century have increased species diversity. Wood extraction at the stand level was positively correlated the relative abundances of *Fagus* and Picea, two economically important species, and it was unaffected by species diversity. However, species diversity might affect the growth of individual trees, leading to shorter time to harvestable dimensions. Besides, the increased costs of diversity associated with planting and management might be compensated by a decrease in the financial risks induced by the low resistance of pure stands to disturbance.

Introduction

Forests cover 30% of the earth's land area, and are home to 80% of our terrestrial biodiversity. Trade in forests products is estimated at more than 300 billion dollars per year (FAO 2010a). They provide humanity with essential services that are cultural, economical (food, medicine, fuel, fibers…) and ecological (biogeochemical cycling, water and air filtering decomposition…) ("Millennium Ecosystem Assessment" 2005; Naeem *et al.* 2009). Wood production is of special importance because we are reliant on it for timber and paper, and because carbon sequestration mitigates

emissions of greenhouse gases (Thompson *et al.* 2009). Sadly, forests, like most ecosystems, are threatened by human activities and their biodiversity continues to decline (Rands *et al.* 2010; Hooper *et al.* 2012). Ninety seven per cent of the total forest area in Europe (excluding Russia) is managed by humans ("Global Forest Resources Assessment 2010" n.d.). To sustain those services, it is crucial to understand how management practices affect the services that forests provide.

Forests are managed to maximize the production of wood used for construction, fuel, or fiber products (Burger 2009). Today still, 30% of European forests are designed for wood production, and only 12% for the conservation of biodiversity (FAO 2010a). Whether mixing tree species improves stand productivity has been a long debated in forestry, and the dominant opinion has changed with time. Though in the 18th century pure stands were thought to be more productive, the in the 19th century the planting of mixed stands was encouraged (Pretzsch & Schütze 2008; Burger 2009). In the 20th century, the results of the first experimental forestry research stations showed that some species like spruce, pine, and fir were more productive in pure stands, but also that productivity depended on site richness (Pretzsch 2009). Today, this topic is still debated, and monocultures are still planted as they are easier establish and maintain (Spiecker 2003). Moreover, the timber industry has adapted its technology (e.g. sawmills) to certain tree species (Truhlář 1997). In 2011, 29% of the European managed forests contained monocultures, 51% contained two or three species, and only 5% had more than six species (FOREST EUROPE *et al.* 2011).

The increasingly rapid loss of biodiversity observed in terrestrial ecosystems has led researchers to explore the relationship between biodiversity and ecosystem functioning. Twenty years of experiments

carried out in grasslands have shown that complementarity for resources between species makes resource-rich sites more productive (Cardinale *et al.* 2011). Forest ecosystems have been less frequently investigated, and although similar biodiversity-productivity relationships may occur, the results are far from conclusive (Thompson *et al.* 2009; Nadrowski *et al.* 2010; Cardinale *et al.* 2011). For example, the relationship between species diversity and forest productivity can be dependent on site richness (Belote *et al.* 2011) or forest type (Paquette & Messier 2011; Vilà *et al.* 2013). Tree diversity can promote productivity through an increase in tree density (Barrufol *et al.* 2013) or through enhanced individual tree growth (Vilà *et al.* 2013). Evidence on the effects of tree diversity on forest functioning comes from two types of investigations: planted experiments similar to the grasslands experiments, and inventory data. Both have their strengths and weaknesses (Nadrowski *et al.* 2010), but neither of them is really suitable to understand how tree diversity in managed forests affects productivity.

The "Training Forest Enterprise", a ten thousand hectare forest located 20 km north of Brno in the Czech Republic has been owned and managed by the Mendel University in Brno since 1923. It has been managed for commercial timber production since 1841, though today it is used for both practical training in forestry as well as commercial endeavours (Truhlář 1997). In the 19th century, when the primary commercial demand was for firewood, most stands were cut at a very young age. Many deciduous tree species, especially oak, were managed by coppicing, a silvicultural practice that takes advantage of the ability of some species to grow from the stump or the roots when cut down. Coppiced oaks grow much faster than if they are planted or naturally regenerated from seed, since they use the old root system (Matula *et al.* 2012). At the end of the 19th century, charcoal was gradually replaced with

coal, and forests started to be mostly used to produce timber for construction, and management practices shifted from coppicing to favouring high forests (Truhlář 1997). Conifers, especially spruce (*Picea abies*) and pine (*Pinus sylvestris*), were widely planted in monoculture since these fast-growing species are inexpensive to plant and maintain. However it soon became clear that they were very sensitive to wind, drought, snow and pests, especially in monoculture. Foresters started to realize that mixing conifers with broad-leaved species improved forest long-term stability (Cotta 1828; Truhlář 1997; Spiecker 2003; Knoke *et al.* 2007). Gradually in the 20th century, new management practices were integrated, such as "green tree retention", i.e. the growing of recruits under the canopy of mature trees (Liira *et al.* 2011). Stand-level clear felling was no longer the unique logging procedure, and small clear-cuts or individual tree removal were applied, especially to introduce conifers into deciduous stands. This was done to increase heterogeneity in forests to make them look more natural, and also because foresters realized that pure conifer stands were much more prone to disturbances. In the second part of the 20th century, the overall composition of the Training Forest Enterprise shifted toward more oak, beech, and larch, and less spruce, pine, and fir. Simultaneously, the successive scientific coordinators established forest stands for various research projects; one of them being the study of wood production and stability in mixed forest stands in anthropogenically changing conditions (Truhlář 1997).

In this contribution, we take advantage of the natural experiment provided by the "Training Forest Enterprise", which contains replicated stands of different species diversity. We chose sites of different tree species richness, going from one to four species, including all possible combinations of *Fagus sylvatica, Larix decidua, Picea abies,* and *Quercus petraea*. Measuring tree diameter and using the number of annual rings to

estimate tree age, we investigated historical management and its effects on wood production. Specifically, we hypothesized that 1) Shifts in management practices have favoured more species-diverse forest stands, and 2) Species diversity positively affects the quantity of wood that can be extracted from forest stands.

Methods

Location

The Training Forest Enterprise extends 49°13' to 49°21'N, and 34°16' to 34°28'E (see Fig 1 in General Introduction). Its altitude ranges from 210 to 574 m above sea level, and the annual mean temperature ranges from 7.5°C at the highest altitude to 8.1°C at the lowest. Average annual precipitation at the highest altitude, lowest altitude, and during the growing season are 685 mm, 528 mm, and 360 mm, respectively. Finally Cambisol is the main soil type, covering 63% of the area (Truhlář 1997). One forest inventory is carried out every ten years, and a rough volumetric composition is estimated for each of the 4000 stands composing the Training Forest Enterprise. Forest type, age, and density are also estimated. All this data is available online (www.mapserver-slp.mendelu.cz/).

Sampling design

Four of the five most abundant species were included in this study: Norway spruce (*Picea abies*), European larch (*Larix decidua*), Sessile oak (*Quercus petraea*), and European beech (*Fagus sylvatica*). From the website, we selected potential candidate sites with volumetric composition matching all possible combinations of these four species. These 15 different compositions were replicated three times, so that total sampling design encompassed 45 sites (See Table 1 in General

Introduction). After an initial survey, sites were selected according to the following criteria: slope < 10% and species composition as recorded in the Mendel University DataBase. In the end, our sites covered a total area of 11 ha; they ranged from 0.07 and 0.6 ha and were 0.24 ha in average. Their altitude ranged from 312 to 579 m a.s.l., and the density of canopy trees ranged from 32 to 81 m^2 of basal area (BA) per hectare. In order to have the same number of individual trees targeted in every composition, we chose six trees per species per site. Thus in monocultures, six trees were targeted, whereas the four-species mixtures included 24 target trees. The target trees were separated by at least 7 m, and spanned the variation in size present at each site.

Data collection

All target trees and their neighbours in a 10 m radius that reached a DBH of 10 cm (Diameter at Breast Height, at 1.3m) were mapped with the Field-Map technology (IFER, Ltd., Jílové u Prahy, Czech Republic; Hédl et al., 2009). For every tree mapped, its spatial position (x-,y-, and z-coordinates) was measured, a species was assigned, the DBH was measured, and its health status (dead or alive) was recorded. In total, 8919 trees were mapped. For the dead stumps, an age was approximated and they were assigned to one of the following categories: “cut in the last five year”, or “more than five years ago”. Because diameter was measured at breast height for living trees, and at the base for stumps, we used allometric equations to correct for the tapering of trees. We summed tree BA, and standardized it per hectare, as a measure of site density. We summed the total BA of stumps that were younger than 5 years and standardized it per hectare as a measure of timber removal. Using the data derived from the maps we measured diversity on canopy trees, by estimating the effective number of species, or the number of equally abundant species ($e^{H'}$, H’ being the Shannon index). We chose this measure

because the sites were selected on the basis of tree species richness, but evenness varied widely among sites. The effective number of species takes both aspects into account, facilitating interpretation.

Two cores were taken for each target tree at a height of 1 to 1.2 m. The cores were dried in newspaper, glued on wooden mounts, sanded with a bench belt sander, and measured at the WSL in Birmensdorf, Switzerland. Ring width was measured to the nearest 0.01 mm by scanning at high resolution with the software WinDENDRO (Regent Instruments Inc 2009). The cores were then cross-dated and corrected using the program COFECHA (Holmes 1983). Nineteen of the 576 target trees were removed from the analysis because they were impossible to cross-date, thus 557 were included in our study. Pith was reached for 110 out of the 557 target trees. For trees where the pith was not reached, we estimated the pith offset graphically (Villalba & Veblen 1997). The pith offset ranged from 1 to 37 years and was 4 years in average. With this method we were able to estimate the age of every target tree.

Statistical analysis

Management plans are decided every ten years, but there is no record of their application. To explore whether sites were subjected to different management practices over time, we looked at how the age of individual trees correlated with the species diversity of the stand in which they grew. Although species diversity was the primary criterion for choosing sites, we analysed it here as a response variable, because it is the result of practical management. We predicted species diversity at the site level as a function of tree age and species identity in a general linear model framework. To see if the evolution in management practices differed

depending on the target tree species, we compared models with only additive or with interacting main effects:

Species Diversity ~ Species Identity + Tree Age (1)

Species Diversity ~ Species Identity * Tree Age (2)

We used the AIC for model selection following the approach of the software writers (Pinheiro & Bates 2009; Crawley 2012). All models were fit in R-3.0.2. (R Development Core Team 2011).

To understand what affected the quantity of timber that can be extracted per unit of area, we used total basal area of timber removed in the past five years per hectare as a response variable. We fitted generalized linear models with a Gamma distribution of errors and a log-transformation of the response variable, to fit the assumptions of normality and homoscedasticity. We fitted models against all combinations of species diversity, tree density, and relative abundance of each of the focal species. We allowed interactions between species diversity and the relative abundance of each focal species, as well as interactions between tree density and the abundance of each focal species. Starting from the most complicated model:

Timber removed ~ Diversity*(%Fagus + %Larix + %Picea + %Quercus)
+ Density*(%Fagus + %Larix + %Picea + %Quercus) (3)

We used the function stepAIC() from the package “MASS” to remove non-significant explanatory variables in a stepwise procedure.

Results

Historical management

To examine the temporal changes in management techniques, we predicted species diversity from tree age and species identity. We found the model with the interaction between tree age and species identity (2) to have a much better AIC than the one without the interaction (14 points difference in AIC). The slope of the regression between species diversity and tree age was negative for all species but *Larix decidua,* for which the slope was not significantly different from zero (Fig. 1). A negative slope indicates that younger trees were found in sites of higher species diversity, and older trees in sites of lower diversity. Our model predicts that given the average diversity of stands where *Fagus* is found today, one would have to go back 113 years into the past [95% Confidence Interval: 65 – 444 years] such that this mean diversity was reduced by one (Fig. 1A). Similarly, one would have to go back 78 years into the past for *Quercus* [95% CI: 65 – 97 years] (Fig. 1C), and 73 years for *Picea* [95% CI: 50 – 137 years] (Fig. 1D) to find them in stands with a mean diversity reduced by one. *Larix* on the other hand, showed no trend: the slope was not different from zero, and the intercept was 2.5 (Fig. 1B). This indicates that larch has always been mostly planted with one or two other canopy tree species.

Effect of management on timber removal

The model chosen by the stepwise selection predicted timber removal by the abundances of *Picea* and *Fagus*, tree density, and the interaction between tree density and the abundance of *Fagus* (Fig. 2):

Timber removal ~ %*Picea* + %*Fagus* + Density + Density:%*Fagus* (4)

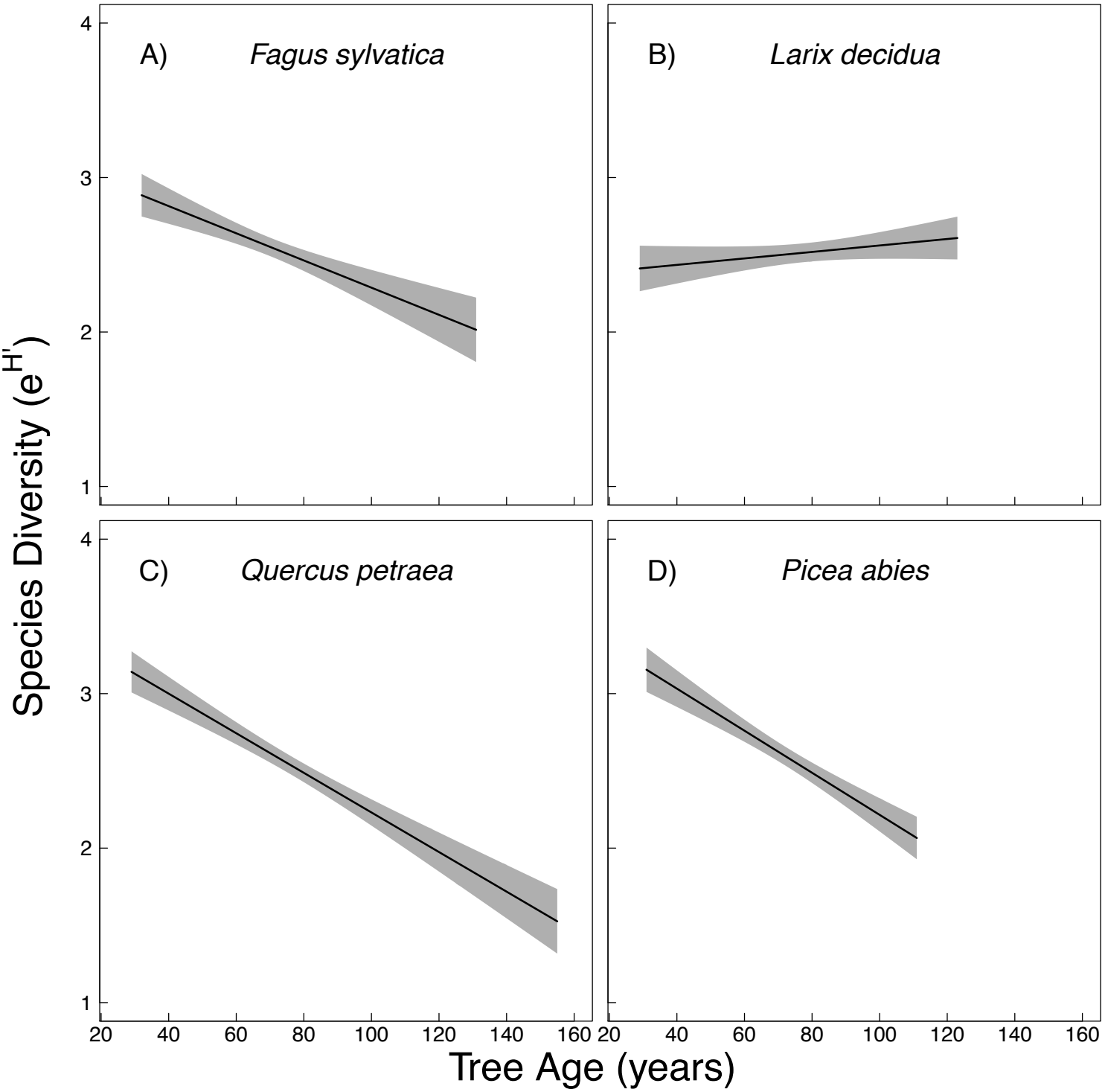

Figure 1: Species diversity ($e^{H'}$) as a function of tree age (years) for all species. The black lines show the mean predictions from the general linear model (see text) and grey shaded areas their 95% confidence intervals.

When the abundance of *Picea* increased from 40 to 60%, the extracted timber increased by 2.7 $m^2.ha^{-1}$ in five years, independently of the abundance of *Fagus* and tree density (Fig. 2A). The effects of tree density and the abundance of *Fagus,* on the other hand, depended on each other.

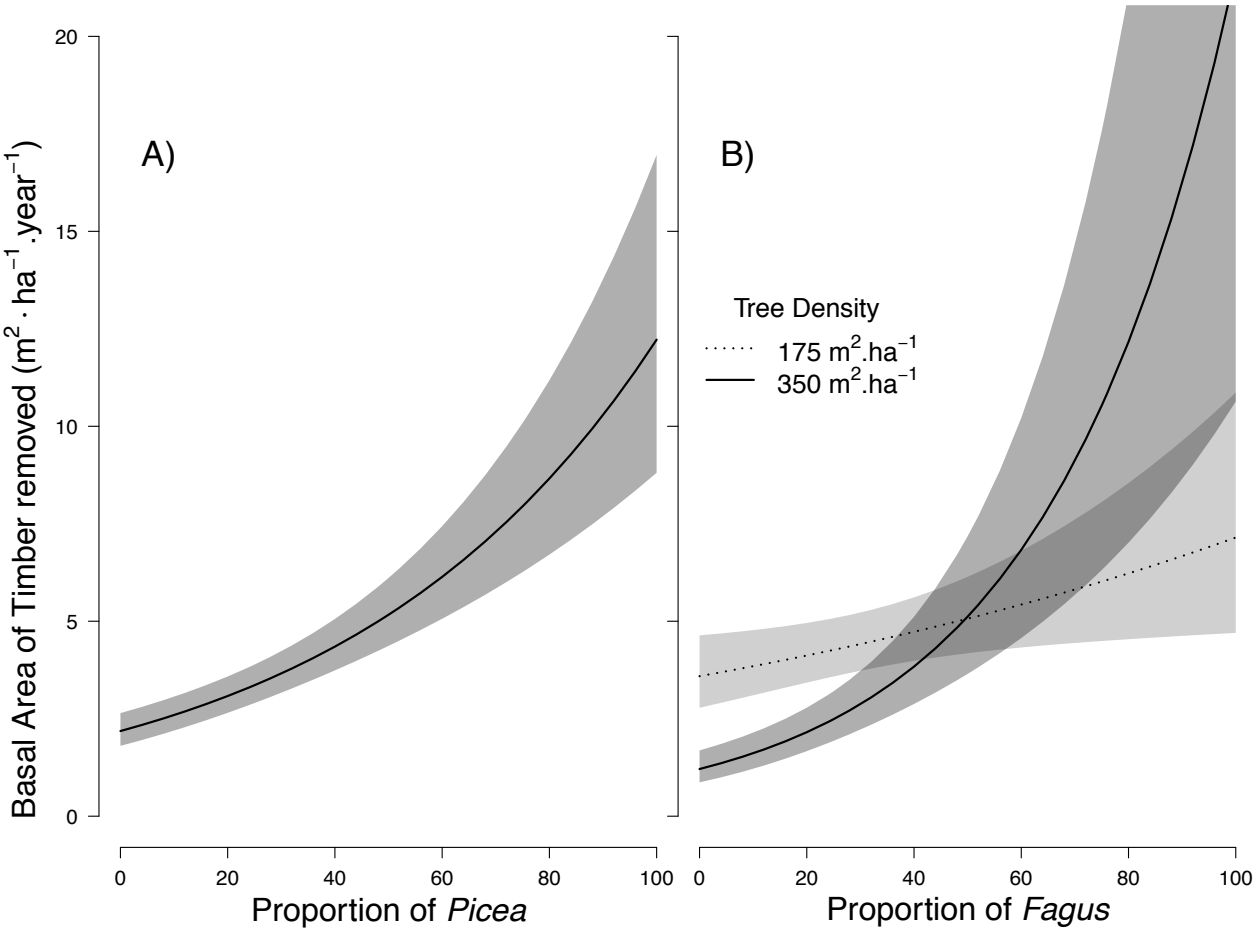

Figure 2: A) Wood extraction (in basal area removed per hectare and per year) as a function of the relative abundance of *Picea* when the abundance of *Fagus* is set to 0% and density to its mean value (255 $m^2.ha^{-1}.year^{-1}$). B) Wood extraction as a function of the relative abundance of *Fagus*, interacting with tree density, when the abundance of *Picea* is set to 0%. The black lines show the mean predictions of the linear model used (see text) and the grey shaded areas show the 95% confidence intervals around the mean.

When tree density was set to its mean value (255 $m^2.ha^{-1}$) and the abundance of *Picea* set to 0%, an increase in the abundance of *Fagus* from 40 to 60% enhanced timber removal by 1.7 $m^2.ha^{-1}$. Similarly, when the abundances of *Fagus* and *Picea* are both set to their mean values (25%), an increase in from 200 to 300 $m^2.ha^{-1}$ in density reduces timber removal by 1.6 $m^2.ha^{-1}$. However, the effect of tree density on timber removal was very dependent on the abundance of *Fagus*, to the extent that the direction of the effect could go from negative to positive. As seen on Fig.2B, when the abundance of *Fagus* is not set to 25% but 75%, the same increase in density increases timber removal by 3.7 $m^2.ha^{-1}$ instead of decreasing it. The effect of *Fagus* on timber removal was also dependent on tree density, but was always positive. At low density (175 $m^2.ha^{-1}$), an increase from 40 to 60% in the abundance of *Fagus* enhanced timber removal by 1.1 $m^2.ha^{-1}$, when at high density (350 $m^2.ha^{-1}$), the same increase in the abundance of *Fagus* enhanced timber removal by 4.6 $m^2.ha^{-1}$ (Fig. 2B).

Discussion

In this contribution, we took advantage of the natural experiment provided by the Training Forest Enterprise, a managed forest in the Czech Republic, and selected sites corresponding to all possible combinations of four economically important tree species. By combining highly precise mapping technology with dendroecology, we were able to get good estimates of site diversity and individual tree age. Because these forest stands were planted at different times, they covered a natural range of tree age and density. Our study design thus allowed us to travel back in time to infer historical management, and to assess the practical effects of management on timber production.

First, we considered species diversity as a response variable, being a result of management practices. We looked at the age of individual trees to travel back in time and see if those trees were found in sites of different diversities. Overall, younger trees were found in sites of higher species diversity, indicating that mixing tree species has become more common over the last century. However differences were found among focal species in these trends, reflecting differences in the silvicultural treatments that foresters apply to them. For instance *Larix* is normally not planted in monocultures, because it branches strongly when it is grown on its own. Foresters usually grow it with at least one other species, because competition for light pushes larch to grow taller with fewer side branches, producing more valuable timber (Truhlář 1997). This explains why *Larix* was the only species for which diversity did not changed through time (Fig. 1B), because since they were always seen as mixtures they were not a focus for further increase in diversity. All other species gradually stopped being grown in pure stands for different reasons, explaining why we observed this negative trend of species richness against age (Fig 1A, C, and D). The most striking example is the one of *Picea*. Because it grows so fast and quickly reaches harvestable dimensions, *Picea* was extensively planted in pure, even-aged stands. But *Picea* is intolerant to drought, and the Training Forest Enterprise is outside of its natural range. When it is weakened by drought, *Picea* is more sensitive to bark beetle and *Armillaria* fungal outbreaks (Truhlář 1997; Jankovsky *et al.* 2004), inducing large die-outs, or at least damaging the wood from inside and making it unsuitable for industrial purposes. Conifers are especially sensitive to pests when they are grown in monocultures, and more resistant when planted in mixtures (Jactel, H Brockerhoff, E Duelli 2005).

We used timber removal as a proxy to evaluate the effect of species diversity on the economic outcome of wood production. Timber removal

was positively affected by the relative abundance of *Fagus* and *Picea*, as well as by the positive interaction between site density and the relative abundance of *Fagus*. *Fagus* and *Picea* represent 6 and 63% in volume of the growing stock in Czech forests (FAO 2010b), and are the main deciduous and conifer species used by the wood industry. In the Czech Republic in 2004, *Fagus* accounted for 30 to 65% of all the non-conifer, industrial wood exported, and *Picea* (together with *Abies*) for 80-90% (UNECE 2004). The data complied by the Economic Commission for Europe (UNECE) pooled the results from spruce and fir, but in the Czech Republic, those two species represent a total growing volume of 470 000 m^3, 98% of which is *Picea.* The positive interaction between density and the abundance of *Fagus* showed that when this species is planted at high abundance and density, its positive effect on timber removal is even greater, which is not the case with *Picea*. *Fagus* is very efficient at capturing light (Chapter 4), so that it might not be as affected by intraspecific competition as the other species, and thus be able to maintain its contribution to stand productivity at high densities (Plauborg 2004; Hein & Dhôte 2006). Our proxy for wood extraction has limitations, the most important being that it applies only for the past five years, and thus reflects only very recent forestry practices. But it already gives us a good idea of what influences timber removal, and especially, it informs us that foresters take most wood where the most economically important species occur. This result also indicates that at the stand level, species diversity has no effect – neither positive nor negative – on wood extraction.

Conclusion

Modern forestry, while still expected to be economically feasible, also has to be ecologically viable and socially acceptable (Burger 2009), and sustainable forest management emphasizes biodiversity conservation (Spiecker 2003). Here we show that in a managed forest in the Czech

Republic, forestry practices have evolved over the last century to answer these societal demands, by increasing tree diversity (Fig. 1). We also demonstrated that the quantity of wood that can be harvested per hectare of forest was not affected by species diversity, but rather increased with the relative abundances of *Fagus* and *Picea,* the most economically important broad-leaf and conifer species in Europe (Fig. 2). However it is important to note that the greatest part of the timber extracted is used for construction, for which a certain wood quality is expected. Large trunks are often required, so that the size of individual trees is as important as stand productivity, and species diversity has sometimes been reported to promote individual tree growth (Vilà et al., 2013, Chapter 2). Besides, when including risk costs into forest economic models, it was proven that mixed stands being more resistant to disturbances, they might actually be more valuable financially (Knoke *et al.* 2007).

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Chapter 2

Tree growth increases with species diversity in a central European forest.

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Abstract

The alarming rate of on-going, anthropogenically-induced biodiversity loss has encouraged a great research effort in understanding how biodiversity affects ecosystem functioning. Most of the evidence comes from fast growing systems, and although forests provide essential services to humanity, they have been much less investigated. Here we combine dendrochronological measurements of radial growth and highly precise mapping technology in a replicated design to explore the effects of diversity on individual tree growth, and its associated temporal variation. We find that species diversity enhanced growth, in such a way that individual growth rates increased by 18 to 28% when species diversity increased from one to four species. Although species had different average growth rates, they benefitted from diversity in the same way, suggesting that complementarity drives the net biodiversity effect in this forest. Individual tree growth was more stable through time in sites of higher density, indicating that intraspecific competition might hinder the variation in radial growth that is due to climate. Our results suggest that in addition to the aesthetic merits and hedging against adverse effects from mono-specific losses due to e.g. disease or climate change, increased forest biodiversity will serve to enhance the supply of natural resources.

Introduction

One of the greatest environmental changes that our planet endures is the loss of biological diversity, which affects the functioning of ecosystems (Rockström *et al.* 2009; Cardinale *et al.* 2012). Forest ecosystems support humanity with services that are essential for its survival and well-being (Gamfeldt *et al.* 2013), among which wood production is of special importance. Trees not only provide timber for energy, construction, or paper, they also directly mitigate the effects of

global warming by transforming atmospheric CO_2 into biomass ("Millennium Ecosystem Assessment" 2005; Naeem *et al.* 2009).

Twenty years of experiments carried out in grasslands worldwide have yielded many insights into the relationship between species diversity and ecosystem productivity (Hooper *et al.* 2005; Cardinale *et al.* 2012). The positive but saturating relationships generally observed indicate that the initial loss of a single species might not have such a strong effect on ecosystem function, but this effect is non-linear and accelerates with the loss of additional species. Higher productivity of diversity rich ecosystems is believed to arise from two processes: the complementarity and the selection effects (Loreau & Hector 2001). Complementarity occurs when resource partitioning or facilitation between species leads to an overall increased resource use. The selection effect is due to the sampling of particular species that affects ecosystem productivity. Positive or negative selection effects correspond to the dominance of species with higher or lower than average productivity, respectively. In terrestrial ecosystems, both processes have been shown to drive the net diversity effect, but complementarity is often regarded to have the stronger influence (Cardinale *et al.* 2007, 2011). Besides, the net effect of biodiversity increases with the number of ecosystem functions considered, and increasing spatial and temporal scales (Isbell *et al.* 2011).

One reason why the diversity effect becomes stronger over time is that "time co-varies with environmental heterogeneity" (Cardinale *et al.* 2011), indicating that considering longer periods of time includes a greater range of environmental fluctuations. Different species reacting differently to environmental fluctuations creates temporal niche differentiation; it is this asynchrony between species that makes diverse communities more stable over time (Loreau & de Mazancourt 2008; Isbell,

Polley & Wilsey 2009; Hector *et al.* 2010) and increases their long term mean productivity (Yachi & Loreau 1999). Single population productivity on the other hand is destabilized by species diversity, because each population interacts with a greater number of species. Since these experiments were carried out in grasslands where individual plants cannot be differentiated, we don't know yet how the variability in the growth of single individuals is affected by species diversity. We can only speculate that similarly to populations, individuals are destabilized by diversity because of more interspecific interactions. Altogether, these results from grasslands suggest that species richness increases ecosystem productivity and stability, and that these effects are actually underestimated when looking at only one function, short periods of time or small areas (Cardinale *et al.* 2011; Isbell *et al.* 2011).

In comparison to grasslands, forest ecosystems have been less frequently investigated, and although similar influences of biodiversity have been suggested, the results are far from being conclusive (Thompson *et al.* 2009; Nadrowski, Wirth & Scherer-Lorenzen 2010; Cardinale *et al.* 2011). For example, the relationship between species diversity and forest productivity can be dependent on site richness (Belote *et al.* 2011) or forest type (Paquette & Messier 2011; Vilà *et al.* 2013), and enhanced productivity has even been found to be driven more by species evenness than by richness (Zhang, Chen & Reich 2012). Tree diversity was also sometimes shown to promote forest stand productivity through an increase in tree density rather than through enhanced individual tree growth (Vilà *et al.* 2013). Evidence on the effects of tree diversity on forest functioning comes from two types of investigations: planted experiments similar to the grasslands experiments, and inventory data. Both have their strengths and weaknesses (Nadrowski *et al.* 2010). Planted experiments can include a broad gradient of species richness replicated with different

species (Scherer-Lorenzen *et al.* 2007; Healy, Gotelli & Potvin 2008; Hector *et al.* 2011), and trees are regularly measured, allowing for precise estimations of their growth rates (Potvin & Dutilleul 2009). These experiments however, are very young and thus insufficient to understand the processes driving productivity in mature forests (Nadrowski *et al.* 2010). Inventories on the other hand, provide data on older forests that are more suitable for exploring such questions (Vilà *et al.* 2003; Paquette & Messier 2011). But these established plots often cover a dilution gradient (Nadrowski *et al.* 2010), where one species is always present (i.e. the matrix species, often *Fagus sylvatica* in Europe), and the only one found in monocultures. Additionally, environmental heterogeneity is often not accounted for, potentially biasing the effects of diversity on productivity (Healy *et al.* 2008). Finally growth is calculated on diameter increment measured every five to ten years only, and the necessary data to consider effects of tree age on radial growth are generally not available from large-scale monitoring efforts. In contrast to grasses, trees can be individually examined, and precisely measuring tree growth is a critical step towards the understanding of what affects it. However it is not straightforward since trees are such large and long-lived organisms. Fortunately in temperate zones, species carry out most of the photosynthesis during the growing season, and they record this cambial growth in annual rings (Speer 2012; Bowman *et al.* 2013). Whereas height growth tends to be rapid at first and then slow dramatically, radial growth is more consistent, and can even be considered linear over short periods of time (Bowman *et al.* 2013). Using annual ring width as a proxy for annual growth appears to be a good way to explore the effects of diversity on individual tree growth (Nadrowski *et al.* 2010).

In the present study, we took advantage of established stands in the experimental forest of the University of Brno in the Czech Republic that

contain different tree diversities to examine the effects on ecosystem functioning. We chose sites of different tree species richness, going from one to four species, including all possible combinations of *Fagus sylvatica, Larix decidua, Picea abies,* and *Quercus petraea*. Using the information contained in annual rings, we investigated the effects of current site diversity on individual tree's past growth. Specifically, we hypothesized that 1) Species diversity positively affects individual tree growth, independently of tree density, and 2) Species diversity increases the temporal variation in individual tree growth.

Methods

Location

The Training Forest Enterprise (TFE) is located north of Brno in the Czech Republic (49°13' to 49°21'N, and 34°16' to 34°28'E), 210 to 574 m above sea level (see Fig 1 in General Introduction), and covers 10,000 ha. The annual mean temperature is 7.5°C, the average annual precipitation 610 mm, and soils are principally Cambisols (Truhlář, 1997). This forest has been managed by the University of Brno for the past hundred years, and is used for both forestry student education and commercial endeavours. Forest type, age, density, and volumetric species composition are estimated in every stand every ten years, and maps on pedology, geology, and topography are also available (www.mapserver-slp.mendelu.cz/).

Sampling design

Norway spruce (*Picea abies*), European larch (*Larix decidua*), Sessile oak (*Quercus petraea*), and European beech (*Fagus sylvatica*) (henceforth referred to by their generic names) were investigated in our study, because they are some of the most abundant and economically important

species in this region. Sites corresponding to the 15 possible combinations of these four focal species were sampled (see table 1 in General Introduction), and replicated three times. This way, every level of species richness (SR), except the highest one, was replicated with different species combinations, and all species combinations were also replicated. Following experimental design recommendations, sites were selected to be as homogeneous as possible in terms of their bedrock, soil type, aspect and slope (Scherer-Lorenzen *et al.* 2005). At each of the 45 sites, six trees of each focal species were targeted, so that six trees were measured in monocultures, and 24 in the full mixtures. In order to have a reasonable record of growth via the tree rings, small trees (<14cm) were not sampled. With this constraint, target trees were chosen in such that they were separated by at least six meters, and that their sizes spanned the range of sizes found at the site. Finally, targets and neighbouring trees (>10 cm DBH) in a 10 m-radius were mapped with the Field-Map technology (Hédl *et al.* 2009, http://www.fieldmap.cz/, General Introduction). This design allowed us to consider every target tree with its neighbours as a block within the site, and to be sure that target trees were independent from each other. Each mapped tree was identified to the species and its Diameter at Breast Height (i.e. 1.3 m, DBH) was recorded. The final sampling design included 45 sites ranging from 0.07 to 0.6 ha, covering a total area of 11 ha, and a total of 8919 trees, 576 of which were targets for detailed biometric measurements.

Data collection

The tree neighbourhood maps were used to calculate tree diversity and density for every site. Tree diversity was calculated as the effective number of canopy tree species, or the exponent of Shannon index ($e^{H'}$), taking both species richness and evenness into account (Magurran 1988; Beck & Schwanghart 2010).

The Shannon index is calculated as:

$H' = -\sum_{i=1}^{SR} p_i \ln p_i$,

where SR is the total species richness, and p_i is the relative abundance of species *i*. Taking the exponent of H' provides an estimate of the number of equally abundant species. H' index increases with SR and with equality in relative abundances. When all species are equally abundant, H' approaches ln(SR), and the effective number of species approaches SR. In contrast, when species composition approaches a monoculture, H' approaches zero, and the effective number of species equals one. Sites were chosen to cover a gradient of SR going from one to four, and the measured values for eSh ranged from 1 to 3.93 (Table 1 in General Introduction). Tree density was defined as the total basal area of canopy trees standardized by area, and ranged from 122 to 425 m^2/ha.

Every target tree was cored twice, at 1 to 1.2 m high. The cores were kept dry in newspaper and glued on wooden mounts. They were then sanded with progressively finer sandpaper with a bench belt sander, and measured at the Institute for Forest, Snow and Landscape in Birmensdorf, Switzerland. Ring width was measured to the nearest 0.01mm by scanning at high resolution with the software WinDENDRO (Regent Instruments Inc 2009). All cores were then cross-dated by species to assign the correct calendar year to each and every annual ring. Crossdating was checked using the program COFECHA (Holmes 1983) and any possible errors were identified and corrected. Nineteen of the 576 target trees were omitted from the analysis because they could not be confidently crossdated. The pith-offset (i.e. number of missing rings and the distance to the pith) was estimated with a graphical method using concentric circles on a transparent sheet when pith was not reached (Villalba & Veblen 1997). With these methods we were able to attribute a year to every annual ring, and thus calculate ages and total diameters. At the time of sampling, target

trees ranged from 29 to 155 years old and 143 to 668 mm in DBH. For every individual, growth curves were obtained as the cumulative sum of ring width over years and averaging measurements from both cores (Fig.1).

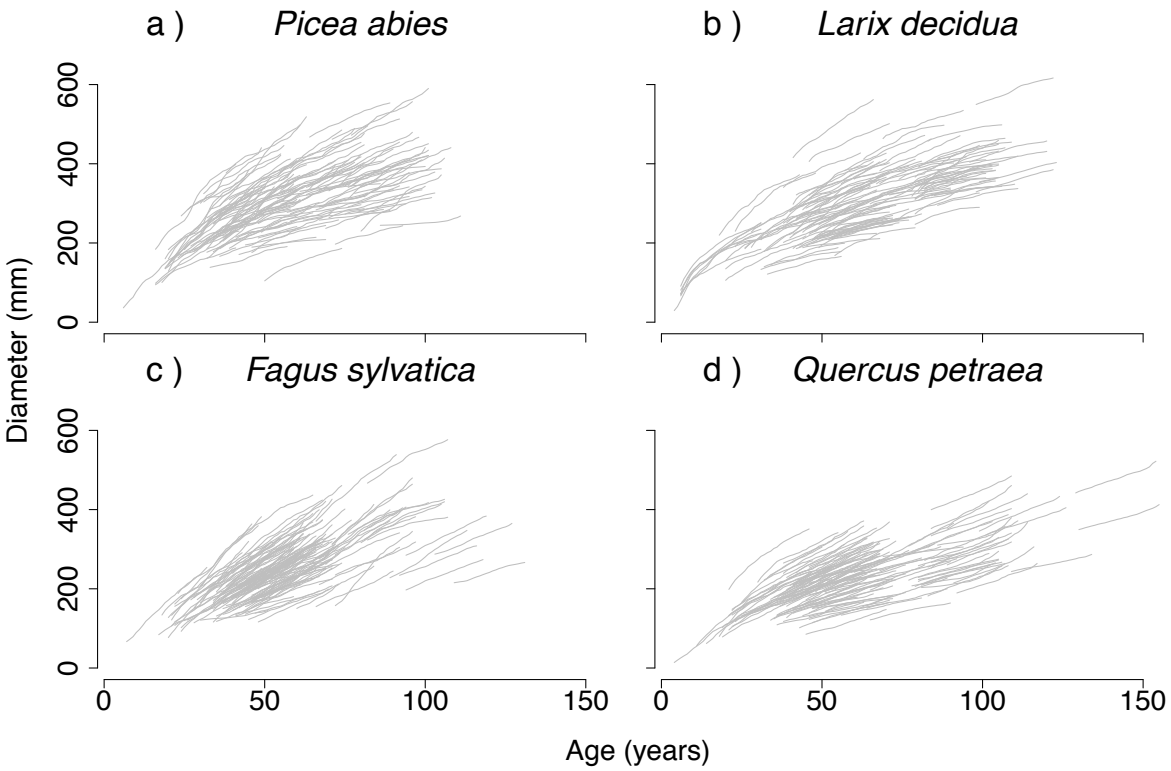

Figure 1: Diameter obtained from cumulating tree ring width series, and plotted against age for every individual of each species. Only the last 25 years of data are shown.

Statistical analysis

Although we have long time series of growth, with many trees older than a hundred years, tree diversity and density were measured only once in 2011. We chose stands thought to be planted with different species richness and compositions, but records from 30 to 150 years ago are far from perfect and we cannot be sure how the effective diversities in 2011 reflect the changing values over the last 100 years. Stand diversity, density, structure and composition will have been affected by natural

processes and silvicultural management treatments. We thus considered only the last 25 years of growth, fitted a straight line to the growth curve (DBH vs age) for every individual (growth during this period was approximately linear), and took the slope of these fits as our estimates of growth (Paine *et al.* 2012). We log-transformed the data as they showed a skewed distribution, and then looked at the effects of species identity, and species diversity in a linear mixed-effect model analysis that also controlled for the expected effects of initial age (i.e. tree's age 25 years ago). We also tested an alternative model with tree density as an additional fixed effect, to test if any effect of species diversity was entirely mediated through this factor or whether additional residual effects of diversity were also present (Barrufol *et al.* 2013).

We calculated the coefficient of variation (CV) for every individual, as defined by the standard deviation of annual radial growth divided by the mean growth. As for individual growth rates and for the same reason, we used only the last 25 years of data. This CV is dimensionless, with lower values indicating more stable individual growth through time. Here again, we log-transformed the CVs to meet distributional assumptions and used linear mixed-effect models to explore the effects of species identity and species diversity after controlling for effects of initial age, and tree density.

For both analyses, site identity was included as the random effect to account for variation between species growth at every site including that due to abiotic features. All models were fitted in R_2.12.0 (R Development Core Team 2011) using the lmer function in the "lme4" package using AIC for model selection following the approach of the software writers (Pinheiro & Bates 2009; Crawley 2012).

Results

Individual tree growth

At the individual level, radial growth rate increased with effective species diversity, with an increase of one species increasing the average growth rate by 0.08 mm year^{-1} (95% CI: 0.01-0.14) (Fig 2c). At average tree age (49 years), increasing the species diversity from one to four species enhanced individual tree growth by 18 to 28%, for the fastest to the slowest growing species.

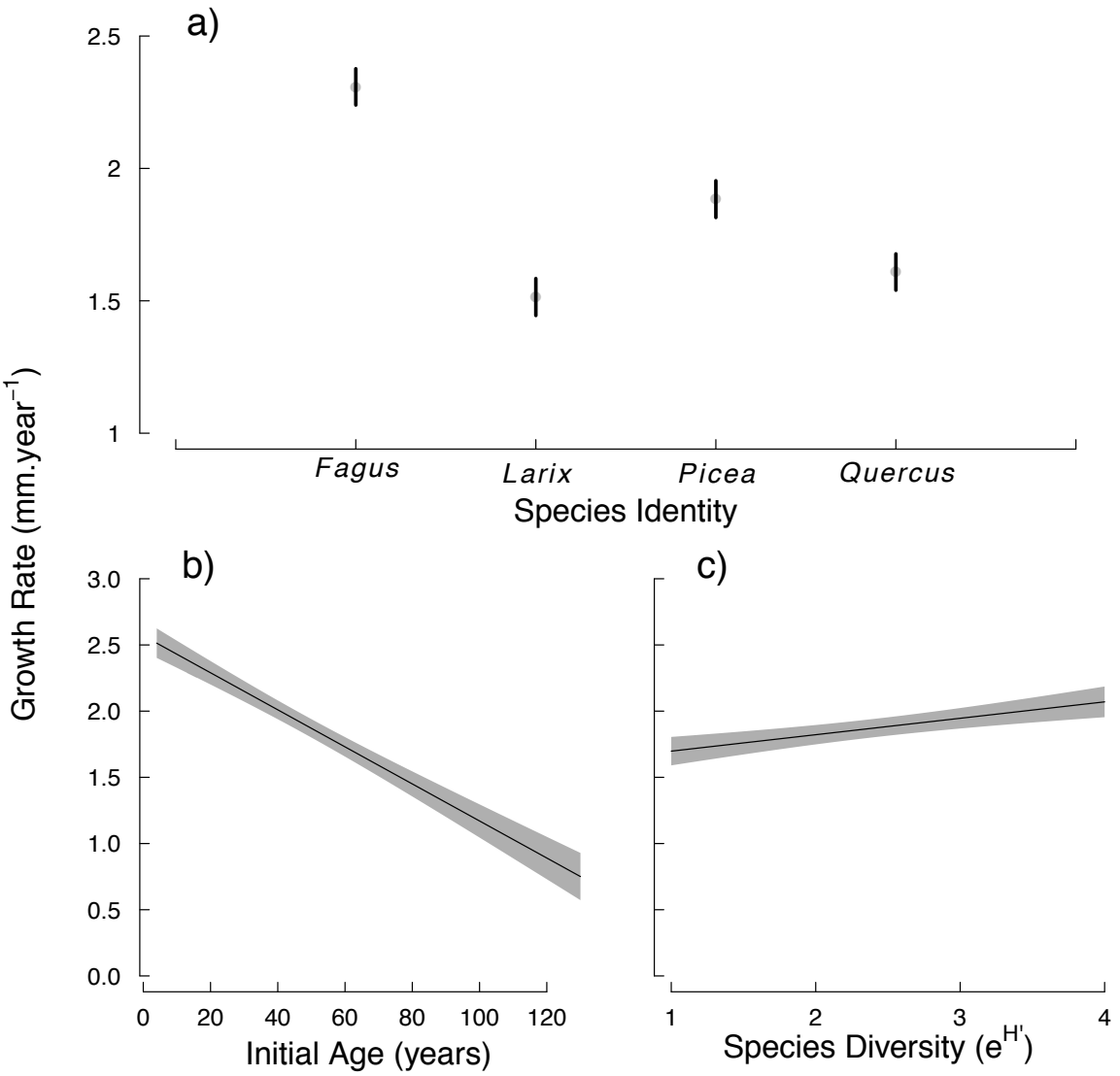

Figure 2: Individual radial growth rates as a function of species identity, tree initial age, and species diversity. The black lines and dots show the fixed effects from the model, keeping all other explanatory variables to their mean values. Bars and shaded areas show the 95% confidence intervals.

Model	Fixed effects formula	Random effects	df	AIC	BIC	Diversity effect: lower bound	Diversity effect: mean estimate	Diversity effect: upper bound
1	log(Growth Rate) ~ Tree Age + Species Identity + Species Diversity	(Species Identity|Site)	17	**490**	**563**	0.013	**0.076**	0.138
2	log(Growth Rate) ~ Tree Age + Species Identity + Species Diversity + **Tree Density**	(Species Identity|Site)	18	**505**	**582**	0.015	**0.077**	0.138
3	log(Growth Rate) ~ Tree Age + Species Identity + Species Diversity + **Species Identity:SpeciesDiversity**	(Species Identity|Site)	20	**504**	**591**	-0.029	**0.067**	0.163
4	log(Growth Rate) ~ Tree Age + Species Identity + Species Diversity + **Species Identity:SpeciesDiversity** + **Tree Density**	(Species Identity|Site)	21	**518**	**609**	-0.021	**0.072**	0.165

Table 1: The different models tested for individual growth rates.

Including tree density in the model didn't improve the fit (the AIC was not lower), and didn't change the effect of diversity on growth rate (Table 1). Growth rate was of course species specific, with *Fagus* being the fastest grower (2.75 mm year^{-1}, 95% CI: 2.61-2.9) at average tree age and intermediate species diversity level (49 years and $e^{H'}$=2.5), followed by *Picea* (2.33, 95% CI: 2.18-2.48), *Quercus* (2.05, 95% CI: 1.9-2.2), and *Larix* (1.96, 95% CI: 1.81-2.11) (Fig 2a). As expected, growth rate decreased with age, but the effect in this case was modest with one-year increase in initial age decreasing the average growth rate by 0.007 mm.year^{-1} (95% CI: 0.005-0.009) (Fig 2b). The model found to best describe individual tree growth included these three fixed effects – species diversity, tree age, and species identity – without any interaction between them. We also fitted a model including an interaction between diversity and species identity to test for a species-specific effect of diversity on growth rate, but the AIC was lower with only additive fixed effects (Table 1).

Temporal variation in individual tree growth

We have no measure of stability at the site level but could analyze the stability of the growth of individual trees. A mixed-effect model with species identity and site tree density as fixed effects best explained the coefficient of variation (CV) in individual tree growth. The higher this CV is, the more variable through time individual tree growth is. *Larix* was the most variable species (0.49, 95% CI: 0.44-0.53), followed by *Picea* (0.45, 95% CI: 0.4-0.5), *Fagus* (0.33, 95% CI: 0.29-0.38), and *Quercus* (0.3, 95% CI: 0.26-0.35) (Fig 3a). The variability decreased with site density, with an increase of 10 m^2 ha^{-1} in density decreasing the CV by 0.009 (95% CI: 0.003-0.015) (Fig 3b). The coefficient of variation was unaffected by species diversity or initial age.

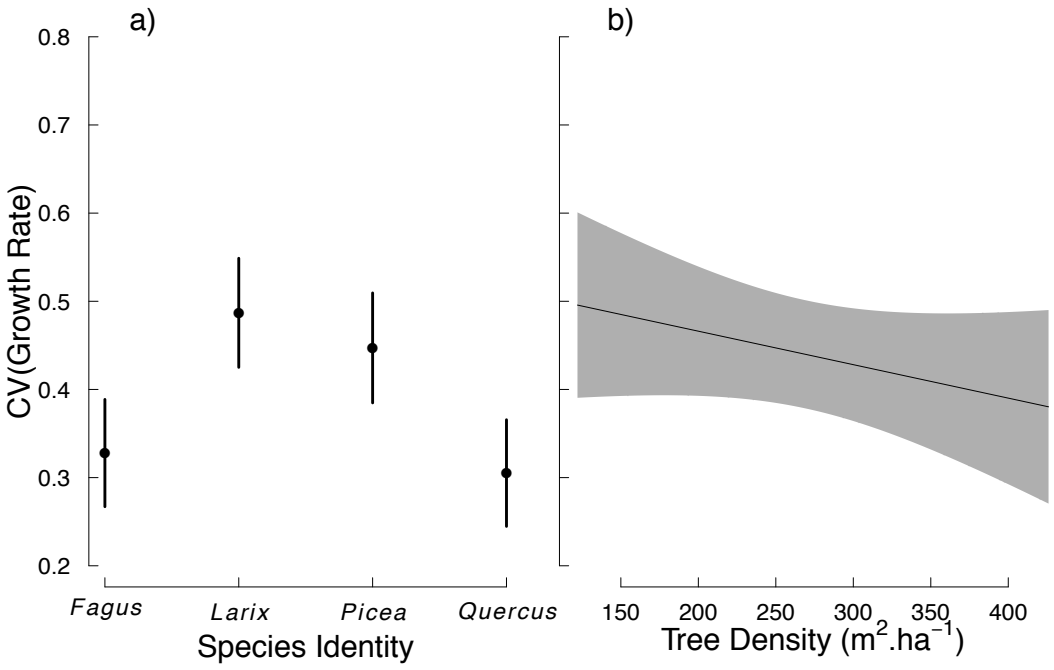

Figure 3: Temporal variation (CV) in individual radial growth as a function of species identity, and tree density. The black lines and dots show the fixed effects from the model, keeping all other explanatory variables to their mean values. Bars and shaded areas show the 95% confidence intervals.

Discussion

Combining dendrochronological methods with highly precise mapping technology, we were able to implement a biodiversity-ecosystem functioning study in a well-established European forest. As most canopy trees are planted and the forest actively managed, tree diversity and composition have been artificially imposed and maintained (Truhlář 1997). Our large dataset of 8900 mapped and measured trees, and additionally annually-resolved growth increments from 576 individuals, collected in a well-balanced sampling design at 45 sites allowed us to assess site- and individual-level characteristics affecting individual tree growth.

We found individual tree growth to be positively affected by species diversity, negatively by tree age, and to be species specific. Increasing

effective species diversity from one to four species enhanced individual growth rate by 18 to 28%. As expected, growth rate decreased with age, in a similar way for all species. Radial growth naturally decreases with size, because a constant diameter increment corresponds to an increasing biomass increment as trees become larger (Pallardy 2010; Speer 2012; Bowman *et al.* 2013). Finally at a similar age and for the same level of species diversity, species had different average growth rates. *Fagus* was the fastest grower, followed by *Picea, Quercus,* and *Larix*. *Fagus* is the most abundant broad-leaved species in Europe, where it grows in a wide range of abiotic conditions, and is often found to be the matrix species (i.e. the species always present, with variable relative abundance, Dittmar *et al.* 2003). Therefore it is not very surprising to see that it grew the fastest at the studied location. The native range of *Picea abies* does not include the Training Forest Enterprise, but it has been widely planted for decades because it is also usually such a fast-growing species that quickly reaches harvestable dimensions. *Larch* and *Quercus* were both slower and had similar average growth rates. Increasing tree density had a negative effect on growth but one that was not statistically significant, and the positive effect of diversity on growth was independent of density effects. Several studies found that forest productivity was increased by an indirect effect of diversity mediated through increased tree density (Paquette & Messier 2011; Vilà *et al.* 2013; Baruffol *et al.* 2013). These studies however, consider only stand-level productivity, so that diversity increases productivity via an increased number of trees, and not via enhanced individual growth. Here we show that the growth of individual trees benefits directly from higher species diversity, as was found by Potvin and Gotelli (2008), in a young tree plantation in Panama.

We found that stand characteristics not only affected growth rates, but also the inter-annual variability in individual tree growth. Our analysis of the temporal variation in tree growth demonstrated that it varied

amongst species, decreased with site density, and was unaffected by biodiversity. Previous studies on the effects of diversity on stability found that the temporal variation in growth increased at the population level and decreased at the community level with increasing species diversity (Yachi & Loreau 1999; Lehman & Tilman 2000; Hector *et al.* 2010; de Mazancourt *et al.* 2013). At first glance our null result appear to contradict with these previous studies. However, it is critical to appreciate that these studies, and the insurance (Yachi & Loreau 1999; Lehman & Tilman 2000) and portfolio effect (Lehman & Tilman 2000) theory that they test, apply at the ecosystem level where asynchronous fluctuations of different species over time buffer the net primary production of the whole system. In contrast, our study only examines the growth of a sample of individual target trees but not the forest stand as a whole. While we found no effect of diversity on the stability of individual tree growth we did detect a stabilizing effect of increasing density. The amount of temporal variation in tree radial growth is known to be tightly linked to inter-annual changes in environmental drivers, especially temperature and precipitation (Babst *et al.* 2013). When trees grow in a denser neighbourhood, they may become more limited by competition than by climatic fluctuations (Cescatti & Piutti 1998). Our findings for reduced inter-annual variability at higher stand densities are consistent with this hypothesis. However if this were the case, and since intraspecific competition is often stronger than interspecific competition (Clark 2010), trees should be less affected by competition overall in stands of higher species diversity where the abundance of each species is diluted. Whether the inter-annual variability in tree radial growth is driven more by environmental fluctuations or by interactions with individuals of diverse species, we expected to see a destabilizing effect of diversity on growth. Maybe one reason why we don't detect this effect is because of the way we measured growth. While a standard and useful measure, radial growth is not without limitations: it decreases with age because basal area increases, and the same diameter

increment translates into different biomass increments for different species depending on their height and wood density (Watt & Kirschbaum 2011; Bowman *et al.* 2013). To improve understanding of how tree diversity impacts forest stability, it may be beneficial to upscale radial growth to biomass growth, using species-specific allometric equations.

Our sampling design didn't allow us to sample all trees in an area in such a way to estimate stand-level stability or productivity. But when individual growth will be calculated from biomass rather than from radial increment, we will be able sum biomass over conspecific trees and have a species-level measure of growth for every site. Similarly, we will sum biomass increment over all trees from a site and have growth estimations at the community level. This will allow us to calculate the relative contribution of the selection and the complementarity effects to the net biodiversity effect with the method from Loreau & Hector (2001). However we can already speculate that in this managed forest of central Europe, complementarity plays a greater role in the biodiversity effect. Indeed we found no significant interaction between the effects of species identity and species diversity on individual tree growth. If the selection effect were strong, we would have expected the effect of species diversity on individual growth to differ amongst species. In particular, we would have expected the more or less productive species to benefit most from species diversity if the selection effect were positive or negative, respectively.

Conclusion

Our study of long-established central European forest stands reveals that those with higher tree diversity had increased growth of all four study species. Our analyses estimate that stands with 4 species have

growth rates increased by approximately 18 – 28 percent relative to monocultures. When managing forests for timber, the total amount of wood that one can harvest per unit of area is of course crucial. However a large part of the timber extracted is used for construction, and thick tree stems are often required for this purpose (Spiecker 2003). Hence various aspects of wood quality are often key considerations in addition to maximising wood production. Furthermore, there are often logistical constraints such as saw mill machinery only being able to handle certain species or size of trees. Nevertheless, our results suggest that tree diversity can have a positive effect on individual tree growth, in addition to the other cultural, aesthetical, and conservation benefits that it holds.

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Chapter 3

Climate response of four co-occurring species in central Europe.

Juliette Chamagne, Lindsay A. Turnbull, Andy Hector, and David C. Frank.

Abstract

Two of the main threats that the Earth is facing in the 21st century are climate change and biodiversity loss. Both may affect the productivity of forests that are the basis for so many ecosystem and societal services. Here we explore the effect of climatic forcing on tree radial growth for four species: *Fagus sylvatica, Larix decidua, Picea abies,* and *Quercus petraea.* Our controlled experimental design, allowed us to investigate if responses to temperature and precipitation of our study species were affected by the tree diversity of the neighbourhoods and stands in which they grew. We found that in this central European lowland forest, all species were most limited by moisture availability as evidence by positive relationships between radial growth and the precipitation during the growing season. Species also differed in this response, with *Quercus petraea* being the most drought-tolerant species, followed by *Larix decidua, Picea abies,* and *Fagus sylvatica* being the most sensitive. These correlations to climate were extremely consistent within species, regardless of the stand species composition and diversity, and could be explained by different functional traits. However these specific differences in the response to climate might in part explain the positive effect of tree diversity on forest functioning. They emphasize the need to better integrate interactions between biodiversity effects and climate change scenarios, if we are to change forestry practices and maintain sustainable forests in Europe.

Introduction

Continuing climate change and increasing biodiversity loss are two of the main threats that the Earth is facing in the 21st century (Rockström *et al.* 2009). Both directly affect ecosystem services upon which the future well being of humanity depends. Scenarios of global change project an overall increase in temperature and precipitation, but these projections, particularly for precipitation, vary greatly in space with high uncertainties over many land areas (Christensen *et al.* 2007). Temperature and

precipitation extremes are also predicted to increase, and dry events are likely to become more frequent. Overall, these climatic changes are hypothesized to decrease forest productivity, potentially reinforcing the release of atmospheric CO_2 (Bonan 2008; Reichstein et al. 2013 Nature) and positive feedbacks within the coupled carbon-cycle climate system (Friedlingstein *et al.* 2006; Frank *et al.* 2010). Species diversity on the other hand, has generally been shown to increase forest productivity (Nadrowski *et al.* 2010; Zhang *et al.* 2012; Chapter 2), but the mechanisms, not to mention applicability across different forest types, remain more heavily debated (Nadrowski *et al.* 2010; Vilà *et al.* 2013). Management practices still tend to favour monoculture stands due to their easier maintenance (FOREST EUROPE, UNECE & FAO 2011). If we are to change forestry practices in order to sustain and optimize the services that forests provide society, we need to better understand how biodiversity and climate affect individual tree growth.

Tree growth and survival depends upon thermal conditions, light, water, and nutrient availability. Therefore, given adequate thermal conditions, competition for light and soil space between individuals limits tree growth the most (Pallardy 2010). But species also differ in the way they use these common resources, because they differ in their physiology, anatomy, and phenology. For example, broadleaved species tend to have longer roots than conifers, with many more orders of branching (Withington *et al.* 2006). Because different species are complementary, to some extent, in the way they use resources, diverse forests are better at exploiting the available resource pool, making them more productive (Nadrowski *et al.* 2010; Zhang *et al.* 2012). Or put another way, conspecific individuals have similar resource use and thus they generally limit each other more than they limit their heterospecific neighbours (Clark 2010). In diverse forests, the abundance of every species is diluted, and so is intraspecific competition. In a previous study, we showed that the radial growth of individual trees increased with species diversity (Chapter 2).

However, we found the temporal variation in individual growth to be unaffected by species diversity, but negatively influenced by tree density. So we wonder if the climate-driven, inter-annual variability in tree growth could be affected by species diversity.

Trees store most of the aboveground carbon in their trunk, and timber production is often regarded as the primary forest function. They of course need to keep investing biomass in roots and leaves to perform photosynthesis. But leaf, root, and wood production are directly related to environmental and biotic conditions (Pallardy 2010; Speer 2012). Variations in radial increment are thus tightly linked to the local temperature and precipitation fluctuations, with exact relationships depending upon species specific characteristics and the climatic conditions at a site (Babst *et al.* 2013). Studying how an individual species respond to climatic forcing in contrasting environments helps understanding its physiology, and what limits its growth. For instance, *Fagus sylvatica* was found to be a very good competitor for light overall, and well adapted to most conditions throughout Europe (Plauborg 2004; Hein & Dhôte 2006). However, comparing *Fagus sylvatica* growth under different climatic conditions showed it to be particularly sensitive to drought at the beginning of the growing season (Lebourgeois *et al.* 2005). If summer drought does increase as predicted, the composition of European forests might shift from being beech-dominated to being dominated by a drought-tolerant species, with significant ecological and economic consequences (Hanewinkel *et al.* 2012).

Studying how different species respond to the same conditions is thus useful to detect how a particular forest might face climate change, and which species are likely to undergo increases or decreases in growth. *Quercus petraea* for example was less affected by drought than co-located *Fagus sylvatica* and *Carpinus betulus* (Leuzinger *et al.* 2005). Similarly,

Larix decidua was found to cope better with drought than *Picea abies* growing in similar conditions (Büntgen *et al.* 2007). In general, is has been broadly known that radial growth is more limited by temperature at high altitude and latitudes, and limited by precipitation at lower altitude and drier sites (Fritts 1976). Recently have these tendencies been extensively quantified across continental-scales in analyses of 36 species from nearly 1000 sites across Europe (Babst *et al.* 2013). These authors calculated correlations between tree ring width and monthly temperature and precipitation time-series, and using a neural network technique dubbed self-organizing maps, clustered sites based upon only their climatic response patterns. Babst et al. (2013) found that these clusters naturally organized by species on the one hand, and by climatic conditions (i.e., temperature-limited versus precipitation-limited locations) on the other hand. In the lowlands of central Europe, tree growth was clearly more correlated to the amount of precipitation, especially to the summer precipitation. Scenarios for global warming in central Europe predict an increase of 2.3 - 5.3°C in temperature, as well as a decrease in summer precipitation (Christensen *et al.* 2007). It seems reasonable to assume that more drought-tolerant species will generally cope better with the predicted climate change. But whether or not species diversity within a forest affects the way plants respond to climate is unknown, although this question is directly relevant to forest management. In a previous study, we showed that the temporal variation in radial growth decreased with tree density (Chapter 2). Since this variation is highly correlated to climatic variation, this result might suggest that in denser sites, radial growth is more limited by competition than by climatic forcing, and thus less variable overall. In sites of higher species diversity, one could hypothesize that intraspecific competition decreases, and trees growth could be more tightly coupled to climatic forcing.

In the present study, we compare the extent to which four coexisting species respond to climate depending on species diversity. We

sampled sites in a lowland central European forest situated in the Czech Republic. We focus on four of the most abundant and important European species: *Fagus sylvatica*, *Larix decidua*, *Picea abies* and *Quercus petraea*, in a replicated design where sites containing all possible combinations of these four species were sampled. Each species was found in eight compositions: in its monoculture, with each of the three other species (three 2-species combinations), with either two of the three species (three 3-species combinations), and in the full 4-species mixture. We explored how trees responded to climatic forcing as a function of the different diversity compositions, and hypothesized that: 1) species respond strongly to the water-limiting environment, 2) species differ in their response to monthly temperature and precipitation, and 3) the strength of the response to climate increases with species diversity.

Methods

Location

The Training Forest Enterprise (TFE) is located in the north of Brno, in the Czech Republic, and extends 49°13' to 49°21'N, and 34°16' to 34°28'E (See Fig. 1 in General Introduction). The TFE ranges in elevation from 210 to 574m above sea level (a.s.l.), and the annual mean temperature ranges from 7.5°C at the highest altitude to 8.1°C at the lowest. With an average annual precipitation of 528 to 685 mm at the lowest and highest altitude, and 360mm during the growing season, this is a water-limited environment, with Cambisol as the main soil type (Truhlář 1997). One inventory is carried out every ten years, and a rough volumetric composition is estimated for each of the 4000 stands composing the TFE. Forest type, age, and density are also estimated. All of these data are available on an online map (www.mapserver-slp.mendelu.cz/).

Sampling design

Four of the most abundant and economically important species were included in this study: Norway spruce (*Picea abies*), European larch (*Larix decidua*), Sessile oak (*Quercus petraea*), and European beech (*Fagus sylvatica*). These will hereafter be referred to by their generic names. From the maps of forest composition, we selected potential sites corresponding to the 15 possible species mixtures, and each of them was replicated three times (see Table 1 in General Introduction). Those 45 sites covered a total area of 11ha, and their altitudes ranged from 312 to 579 m above see level. Six trees of each species were selected at each site, ranging from a total of six trees sampled in the monocultures to 24 in the full mixtures. The target trees were chosen to be at least 7 m apart, and to span the variation in size present at the site.

Data collection

A total of 576 trees were sampled, 144 of each species, and two cores were taken for each tree, at 1m height. The cores were dried in newspaper, glued on wooden mounts, sanded with a bench belt sander, and measured at the WSL, Birmensdorf, Switzerland. Ring width was measured to the nearest 0.01mm by scanning at high resolution with the software WinDENDRO (Regent Instruments Inc 2009). The cores were then cross-dated, with the dating quality verified using the program COFECHA (Holmes 1983). Nineteen of the 576 target trees were excluded from the analysis because they could not be confidently cross-dated, resulting in a total of 557 trees for the final analyses. The individual tree-ring measurement time-series were ranged from 14 to 164 years long (69 years on average). For sampled trees where the pith was not present in the cores, the pith-offset was estimated using a graphical method with transparent templates of concentric circles (Villalba & Veblen 1997). The

pith was hit for 110 out of the 557 target trees, with a four year average pith offset estimate and ranging from 1 to 37 years.

Daily mean temperature and daily precipitation were obtained from the Czech Hydro-meteorological Institute In Brno. The temperature data were transformed into mean monthly data, and the precipitation into monthly precipitation sums. We also averaged monthly temperature and cumulated precipitation in various seasonal window spanning different parts of the growing season.

Statistical analysis

Years with characteristic extreme growth reactions, the so-called pointer years, were identified for all of the species. The raw ring-width measurement time series were pooled by species, regardless of their original plot. Pointer years were defined as years with 75% of all series with radial increments at least 10% larger or smaller than the previous year. Pooling series regardless of site conditions served to identify pointer years driven by common climatic forcing, and not by more local, and plot specific biotic and abiotic factors. Pointer years were calculated in R_2.12.0 (R Development Core Team 2011) for each species separately, with the "pointer" function in the "dplR" package (Bunn 2008).

The raw tree ring series were then pooled by species for each composition, i.e. pooled from the three replicate sites of each species mixture. They were first aligned by cambial age to best evaluate the specific growth trends using the program ARSTAN (Holmes & Fritts 1986). The regional curves (RCs) obtained were analysed for species and composition differences (Fig. 1).

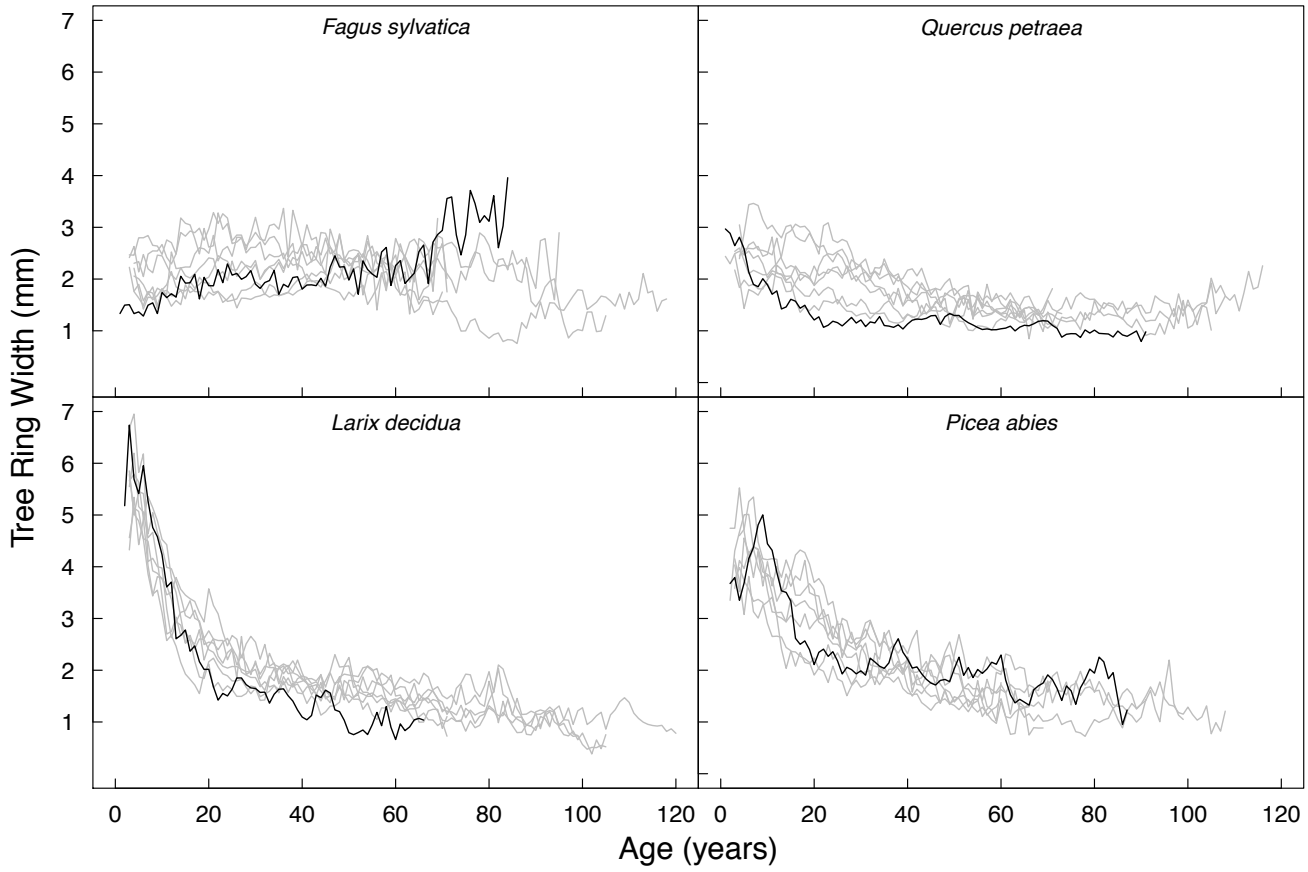

Figure 1: Regional curves (RCs) of the 32 series after aligning them by cambial age. The black lines show each species in monoculture, the grey lines show the different mixtures.

Second, series were aligned by calendar year and individually detrended using a cubic smoothing spline with a 50% frequency cut-off at 60 years (Cook & Peters 1981). This spline allowed us to remove the so-called age trend and other low-frequency variation in the raw series that is due to biological and site effects, and to retain the higher-frequency variation related to climatic variation (Fig. 2). The resulting tree-ring indices were averaged together in the program ARSTAN to obtain a total of 32 species-level chronologies representing the four species for all four biodiversity levels and species combinations.

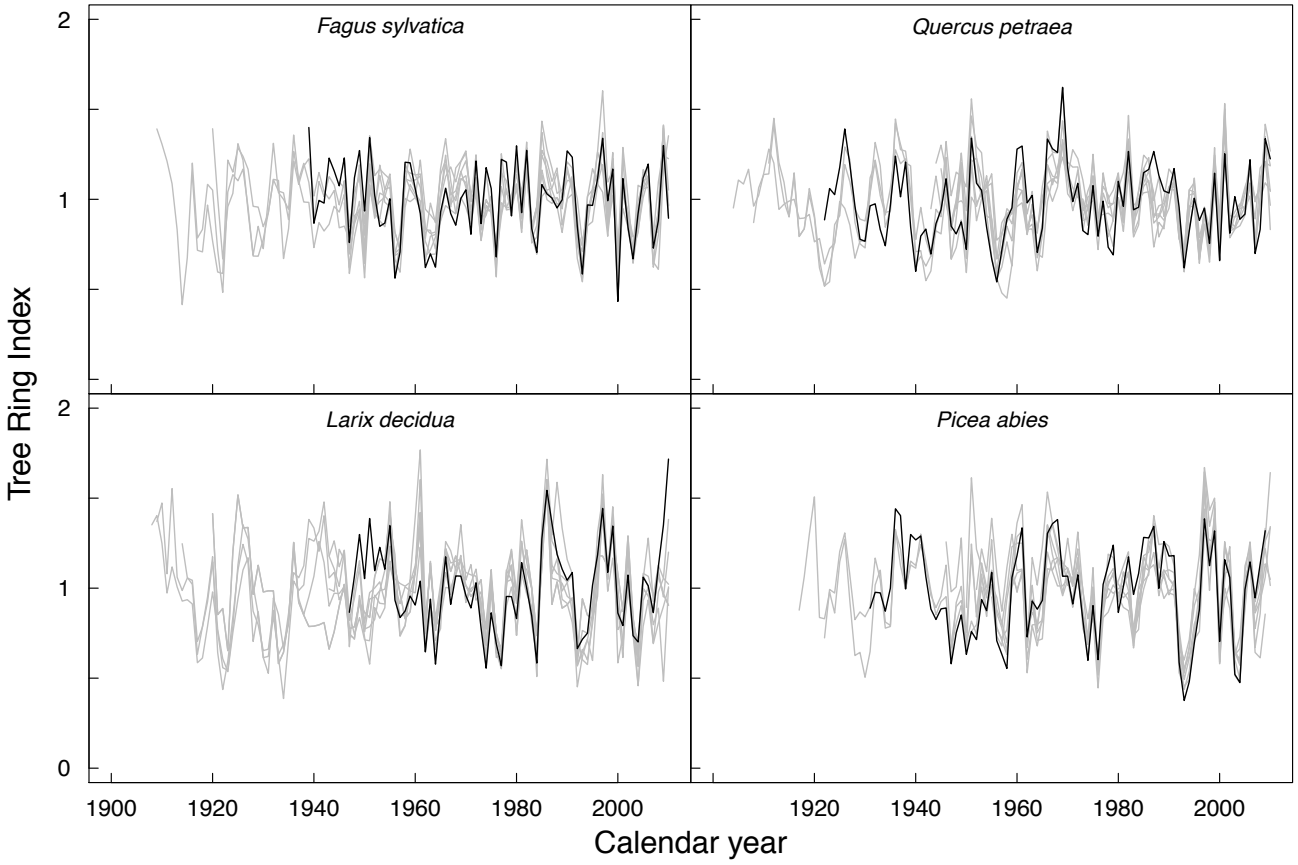

Figure 2: The 32 chronologies after 60-year spline detrending. Tree-ring indices were calculated as ratios from the estimated growth trend curves and series. A tree ring index of 1 indicates no deviation from the growth curve. The black lines show the species in monocultures, the grey lines show the mixtures.

The 32 tree ring width chronologies were related to monthly and seasonal temperature and precipitation by computing monthly climate correlation functions (CCFs) using the Pearson's product moment correlation over the 1954-2009 period. CFFs were computed for all months of the current year and previous year, for the annual mean of the previous year and current year, for April-October, April-July, and August-October means of the previous year, and for April-October, April-July, August-October, May-July, May-June, and June-July means of the current year. The period 1954-2009 was chosen to compute the correlations to

climate because all average series truncated at a minimum of five trees overlapped over this period. As an indicator for the strength of the total climate forcing we took the absolute values of all correlations to monthly means, and averaged them, and also studied the correlation to the period for which species responded the strongest. We then fitted these overall correlations against site species richness in a general linear model framework using R.2_12_0 (R Development Core Team 2011).

Results

Pointer years

The species-level chronologies showed a combination of species-specific and intra-specific common variability and pointer years (Fig 3). Notably, there were four years in the last 100 years where all species showed a negative growth anomaly: 1962, 1976, 1992, and 2000 (Fig. 3I). Otherwise, pointer years were generally common between two or three species, but occasionally unique to one species. *Fagus* was the species with the most pointer years (23, Fig. 3A), followed by *Picea* (22, Fig. 3G), *Quercus* (18, Fig. 3C), and *Larix* (17, Fig. 3E).

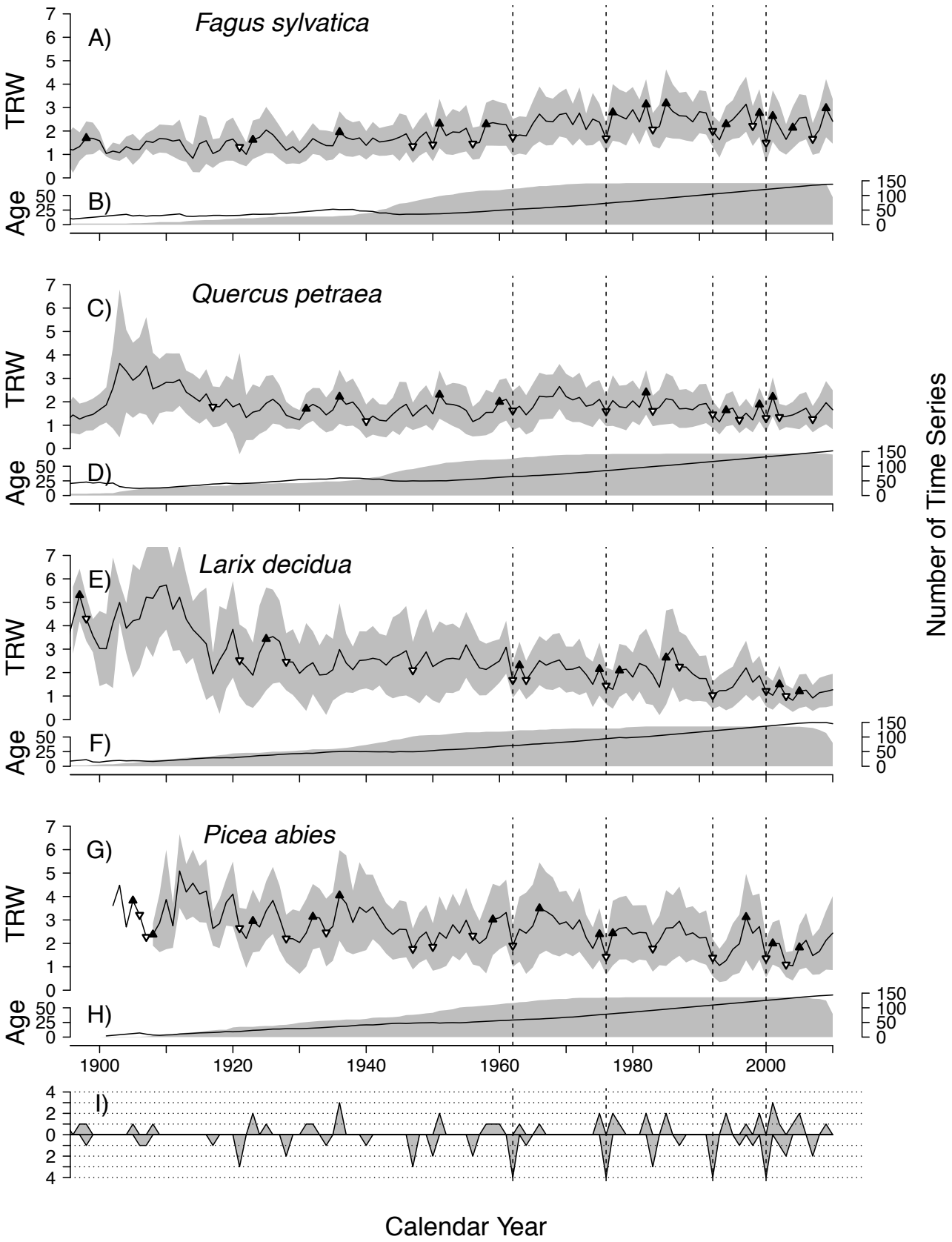

Figure 3: A), C), E), and G) Mean (black line) and standard deviation (grey shaded area) of raw tree ring series. Upper filled triangles, and lower empty triangles show positive and negative pointer years. B), D), F), and H) Mean series age (black line), and number of time series used to compute the average (grey shaded area). I) Summary showing the number of species with positive or negative pointer years.

Fagus was also the only species with more positive than negative pointer years, and shared pointer years mostly with *Picea* and *Quercus*. Pointer years for *Larix* were mostly unique, or shared with *Picea*. *Picea* shared most negative pointer years with *Fagus* and with *Larix*, and *Quercus* with *Fagus*.

Species – specific growth trends

The age-related trends in radial growth obtained from cambial age-aligned series were found to be quite specific to each species (Fig. 1). Both conifers showed very high initial growth rates, decreasing exponentially the first 20 years. During this juvenile growth period, *Larix* decreased from 5.5 to 2 mm per year on average, and *Picea* from 4.5 to 2.5 mm/year. *Quercus* also showed an exponential-like decrease but with more modest changes in radial growth from 3 to 2 mm/year in 20 years. The growth trends observed in *Fagus* tended to be quite small on average, with some series increasing and others decreasing over time. We did not find any consistent effect of species composition or diversity on specific growth trends.

Specific responses to climate

The strongest response to climate identified for all species was a positive correlation to precipitation sums from May to July of the current growing season (Fig. 4A, C, E, G). This late spring- early summer precipitation response was particularly prominent in *Fagus*, *Larix* and *Picea* with values ranging from 0.39 to 0.69. Only half the *Quercus* series had significant correlations to monthly precipitation. All species also showed negative correlations to temperature during the current growing season, but which of these months had the most influence varied among species (Fig. 4B, D, F, H).

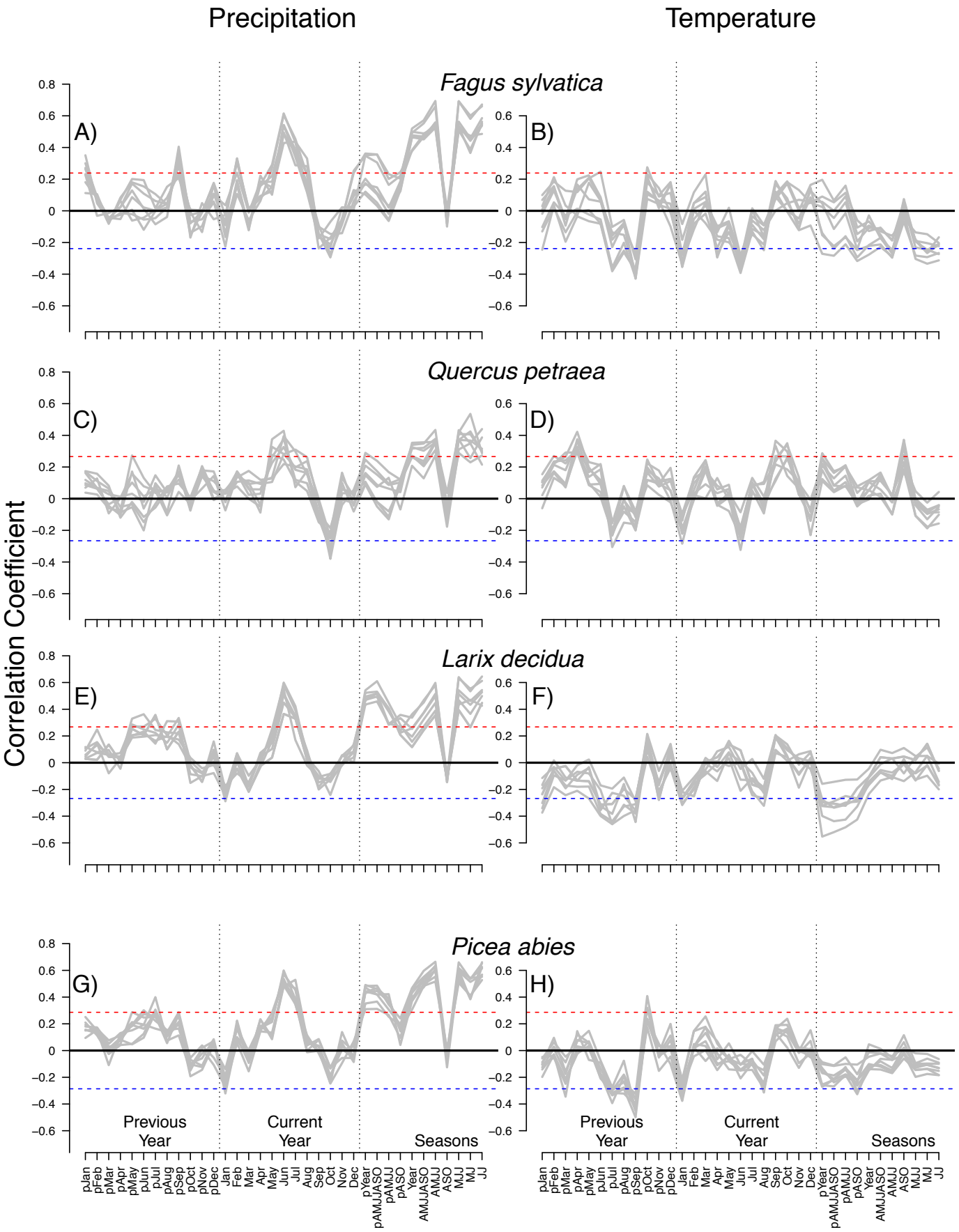

Figure 4: Correlations between tree ring width index and precipitation (A), C), E), G)) and temperature (B), D), F), H)). Correlations above the red threshold show positive significance, those below the blue threshold are significantly negative.

These negative correlations with summer temperature tended to be weaker than the correlations to precipitation, indicating that tree growth is more limited by water. It is also important to note that precipitation and temperature are not independent, so that high temperatures and low precipitations during summer strongly correlate. Negative correlations with June temperatures were most prominent for *Fagus* and *Quercus*, when *Larix* and *Picea* showed strongest responses to temperature in August. Besides, *Quercus* showed a slight positive correlation (for some chronologies) with the temperature in the end of the current growing season (August-October).

Interestingly, while the species showed relatively high similarities in the climate response to current season conditions, influences from the previous years climate was strongly species specific. The two conifer species showed similar responses to the previous growing season. They both correlated positively to the precipitation in the previous April to October, but *Larix* had stronger correlations than *Picea. Larix* also showed a negative correlation with the temperature of the same period, whereas the negative correlation with temperature was found for the previous September for *Picea*. *Fagus* strongly correlated with the conditions in the previous September: it showed a positive correlation to precipitation and negative to temperature. *Quercus* showed a completely different pattern, where the temperature in the previous April had a positive effect on its growth. We found the climate response to be unaffected by diversity, and to be very coherent within species (Fig. 4). Indeed the different chronologies of each species, corresponding to the different compositions they appear in, showed very similar correlations to monthly temperature and precipitation.

Species	Phylogenetic group	Functional type	Rooting system	Phenology	Light demand	Ecological succession
Fagus sylvatica	Angiosperm	Deciduous	Shallow to intermediate but powerful (max depth >1m, max density 0.2-0.5m)	Radial growth initiated 0-10 days after bud burst	Highly shade tolerant	Maintains a high growth rate until late maturity, late successional species
Quercus petraea	Angiosperm	Deciduous	Deep (max depth 2m)	Radial growth initiated 2 weeks before budburst	Intermediate shade tolerant	Intermediate to late successional, slow grower
Larix decidua	Gymnosperm	Deciduous	Shallow (max depth 1m, max density at 0.2-0.3m)	Radial growth initiated 3-6 weeks after needle (and shoot) growth	Light demanding	Pioneer species, one of the fastest growing conifers
Picea abies	Gymnosperm	Evergreen	Very shallow (max density < 0.2m deep)	Radial growth simultaneous to shoot extension	Shade tolerant	Late successional, fast growing species

Table 1: Selected traits related to the biology, phenology, and ecology of the studied tree species.

Discussion

In the present study, we explored how biodiversity affects the response of tree growth to climate. We sampled four economically important species growing in sites of different species diversity, covering a gradient of one to four species. We quantified which climatic elements most limited tree growth in this region, and assessed how climate responses were differentiated among these four species. We also showed that species diversity does not modify the correlation between radial growth and climate.

In the Training Forest Enterprise, a lowland temperate forest of central Europe, we found all tree species to show a positive relationship between tree ring index and total precipitation in the current May to July. This correlation to precipitation was strongest for *Picea*, followed by *Fagus, Larix*, and *Quercus*, for which not all chronologies reached the threshold limit of significance*. Quercus petraea* was previously described as a drought-tolerant species (Leuzinger *et al.* 2005; Friedrichs *et al.* 2009a; b; Michelot *et al.* 2012), and our study supports this evidence with relatively modest correlations between Quercus growth and precipitation variation. Our study also extends upon a recent Europe-wide analysis showing that at low altitudes trees primarily respond to summer precipitation (Babst *et al.* 2013). Tree radial growth also responded negatively to temperature in the current growing season suggesting additional thermal influence contributing to drought stress. However, the inverse relationships between summer temperature and precipitation confound the exact attribution to water availability and thermal controls on evaporative demand. A positive correlation between tree ring index and climate in the past growing season was also detected but varied among species. Such responses to climate conditions in the year prior to ring formation emphasize the importance of delayed effects of water depletion on growth. It is likely that carbon reserves called upon to initiate radial

growth are primarily responsible for such lagged effects (Michelot *et al.* 2012).

Fagus sylvatica had the second highest positive correlation to precipitation in the current May-July (Fig. 4A), and the most negative correlation to temperature in the same period (Fig. 4B). The CCFs suggest *Fagus sylvatica* is the most sensitive species to climate in the current year, as was found by others (Dittmar, Zech & Elling 2003; Friedrichs *et al.* 2009b; Michelot *et al.* 2012). Michelot *et al.* (2012) explained this physiological response by the fact that budburst occurs before the initiation of radial growth for this species (Čufar *et al.* 2008), so that leaves are active and respond to climate prior to ring formation. However it is important to note that *Larix* also has budburst prior to radial growth (Moser *et al.* 2010, Table 1), and is not as sensitive to climate as *Fagus*. *Fagus* was also found in some studies to be sensitive to previous year's drought (Dittmar *et al.* 2003); it is also the case for most series in our study, and we show that drought in the previous September was especially limiting. *Quercus petraea* was the least sensitive species to climate and especially to drought in the current growing season (Fig. 4C-D), corroborating many previous studies (Friedrichs *et al.* 2009b; Michelot *et al.* 2012). We even found it to be positively affected by the temperature in the current August to October, at the end of the growing season. Michelot *et al.* found *Quercus* to be sensitive to last year's water depletion, owing to its development of early wood prior to budburst (Michelot *et al.* 2012). We did not find this pattern here, and some series were positively correlated to high temperatures in the prior April. *Quercus* has much deeper roots than any other studied species (Thomas & Hartmann 1998; Hruska *et al.* 1999, Table 1), probably explaining why this species is not as sensitive to climate, and can even take advantage of high temperatures (Fig. 4D). *Picea abies* was the most sensitive to precipitation in general (Fig. 4G), which supports other studies finding this species to be drought sensitive (Bréda *et al.* 2006; Büntgen *et al.* 2007). *Picea* was found to be more limited by

temperature than *Larix decidua* and *Pinus sylvestris* at a similar altitude in Austria (Schuster & Oberhuber 2012). *Picea* is the studied species with the shallowest rooting system, perhaps explaining its high sensitivity to the water supply (Bischetti *et al.* 2005; Bolte & Villanueva 2005, Table 1). However *Picea* was found to be less sensitive than in *Larix* to the growing season of previous year. Finally *Larix* was shown to be more drought-tolerant than *Picea* but more dependent on the climate in the previous growing season (Fig. 4E-F), patterns consistent with carbon reserves assimilated during this period being used for subsequent bud development (Schuster & Oberhuber 2012). Indeed the needle growth is initiated three to six weeks before radial growth, as was shown by phenology studies (Moser *et al.* 2010; Swidrak *et al.* 2013, Table 1). These results were confirmed by the present study since the overall correlation to precipitation was weaker in *Larix* than in *Picea,* but the positive correlation to precipitation in the past April-August was stronger in *Larix* (Fig. 4 E-H). Altogether, these results show that trees' response to climate are very species-specific, and can be partly explained by some functional traits like rooting depth or phenology (Table 1).

The climate correlations were not affected by species diversity or species composition, and were rather very coherent within species. We know that tree radial growth decreases with increasing competition (Plauborg 2004), and in addition to the total competition as quantified, for example, by stand density, species are usually more limited by their conspecifics (Clark 2010) since they have a similar resource use. Indeed, when species diversity increases, the abundance of every species is in average diluted, and so is intraspecific competition. We thus expected to see a positive effect of diversity on the correlation to climate, reflecting a change from limiting intraspecific competition in low diversity stands, to limiting climate in high diversity stands. However, we considered the effect of species richness only, because we analysed climate correlations at the composition level, pooling tree ring series from sites with similar

composition. It was shown that species evenness greatly affects forest productivity (Zhang *et al.* 2012, Chapter 2), and we might find an effect of diversity if we computed CFFs at the site level, where it is possible to calculate the effective species richness, taking both species richness and evenness into account. However if species diversity destabilizes the productivity of plant populations through time, and stabilizes that of ecosystems (Hector *et al.* 2010), its effect on individual temporal variation has been much less investigated. In a previous study (Chapter 2), we found individual growth to be stabilized by density, so it would be interesting to explore the effects of density, intra- and inter-specific competition on the correlation to climate.

Conclusion

Much uncertainty remains in predicting how forests will cope with biodiversity loss and global climate change. We need to understand how these changes will affect individual tree growth and ecosystem functioning if we want to sustain the services that forests provide society. Here we show that species respond strongly and differently to climate, which could in part explain the complementarity between individual species and thus the overall higher productivity of diverse ecosystems (Nadrowski *et al.* 2010; Zhang *et al.* 2012). Yet, the results of our study will require further expansion and testing. Ideally, the direct and indirect effects of biodiversity on tree growth could be disentangled in a process-based model framework. It seems that many of the effects and biological processes at play may require model development to consider whether growth is initiated before (*Quercus*) or after (*Fagus*) budburst, the role of stored carbohydrates, and the highly complex ways in which species respond to climate variation (Babst *et al.* 2013). The differences we observed for *Quercus* and *Fagus* are notable in a modelling context, as they would usually be considered to belong to the same plant functional type. Besides, our experiment should be replicated in a cold, temperature-limited environment, where global change might have different effects on

tree growth (Christensen *et al.* 2007; Meehl *et al.* 2007; Bonan 2008). Similarly, the effects of management on ecosystem productivity, and influences of confounding environmental factors such as CO2- fertilization and nitrogen deposition will require further attention. But we believe that our study, which combines a replicated sampling design "borrowed" from the fields of biodiversity and ecosystem functioning, and classical dendrochronological methods, already provides a good multidisciplinary approach well suited to answer such challenging questions.

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Chapter 4

Disentangling the effects of environmental conditions, tree species diversity and composition on understory diversity.

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Abstract

Forests are an important terrestrial biome, and not only because they provide us with timber. Understory organisms contribute to the decomposition of plant material, and thus participate in many biogeochemical cycles in forests, especially carbon cycle. Different groups of understory organisms are known to be affected by tree identity and abiotic conditions, but no comprehensive study has looked so far at the direct and indirect effects of tree identity and diversity on those groups. In this study we established transects in forests containing one to four tree species. We collected and measured the diversity of beetles, earthworms and herbs, and analysed the effects of tree diversity and identity on those groups using structural equation modelling. Tree diversity directly promoted the diversity of earthworms and saproxylic beetles, important decomposers of leaf litter. Tree species identity affected understory invertebrates directly and indirectly, via changes in abiotic conditions. *Fagus sylvatica*, for instance, captures light efficiently, and as such affected the understory via its effect on canopy cover, whereas *Quercus petrea* produces easily decomposed leaf litter, and its indirect effects were mediated by reduced humus mass. Interestingly, we found a negative effect of tree diversity on herb diversity, mediated through an increase in canopy cover. This indicates that trees and herbs compete for light, and since competition for light is asymmetric, trees outcompete herbs. While making intuitive sense, this result contradicts some studies, indicating that the positive effect of tree diversity on herb diversity often reported in the literature emerges from abiotic factors that favour both plant strata. Our study suggests that tree species diversity promotes the diversity of several groups of decomposers in the understory, and thereby affects biogeochemical cycling in forests.

Introduction

The relationships between canopy tree diversity and the diversity of organisms in the understory is little known, although soil invertebrates have major impacts on ecosystem processes (Wardle *et al.* 2004; van der Heijden, Bardgett & van Straalen 2008). Earthworms and other soil invertebrates play a crucial role in litter decomposition, a key step in nutrient and carbon cycling in most terrestrial ecosystems (Aerts 1997). They affect plant growth directly by feeding on roots (Scheu 2003), and indirectly by altering soil structure, nutrient availability and the activity of soil microorganisms (Wardle David A. 1999; Scheu 2003; Wurst *et al.* 2003; Partsch, Milcu & Scheu 2006). Although understory herbaceous plants contribute only about 0.2% of total forest biomass (Gilliam 2007), they generate 4% of primary net production (NPP) (Muller 2003). The herb layer also contributes up to 16% of foliar litter (Muller 2003), with greater nutrient content and more rapid decomposition than tree-leaf litter. Therefore invertebrates and herbs in the understory have a significant impact on nutrient and carbon cycling in forests (Yarie 1980; Nilsson & Wardle 2005; Gilliam 2007). So if tree diversity affects the diversity of understory organisms, it indirectly affects nutrient cycling.

In general, tree diversity is considered to have positive or at least neutral effects on the diversity of understory organisms, including earthworms, beetles and herbs (Nadrowski, Wirth & Scherer-Lorenzen 2010). This is usually explained by the differential facilitation effects of each tree species on certain understory species (Augusto, Dupouey & Ranger 2003; Lassau *et al.* 2005), as well as by an increased heterogeneity in the forest floor and soil conditions (Cesarz *et al.* 2007; Sobek *et al.* 2009; Vockenhuber *et al.* 2011), resulting in more species coexisting in the understory. However, evenness of tree species rather than richness was shown to be a key aspect of diversity driving forest functioning (Zhang,

Chen & Reich 2012), and is therefore likely to also be crucial in the effect of tree diversity on understory diversity.

Understory diversity is also affected by environmental conditions and tree identity (Augusto *et al.* 2003; Lassau *et al.* 2005; Mölder, Bernhardt-Römermann & Schmidt 2008). Soil and litter properties have significant impacts on the diversity of earthworms, soil beetles and herb species (Ponge *et al.* 1999; Wardle *et al.* 2004; Vockenhuber *et al.* 2011), whereas light availability often limits herb layer species richness (Kirby K J 1988; Jennings, Brown & Sheil 1999; Hofmeister *et al.* 2009). On the forest floor, soil, litter and light properties are strongly influenced by tree identity, due to inter-specific differences in crown light transmittance, litter chemistry and decomposition rates (Hobbie *et al.* 2006; Barbier, Gosselin & Balandier 2008).

It is evident that tree diversity, tree species identity and abiotic properties affect understory diversity. But no studies published to date have simultaneously explored the effects of these three factors, rending it impossible to determine their relative importance (e.g. Mölder *et al.* 2008; Sobek *et al.* 2009; Vockenhuber *et al.* 2011). Another limitation of previous studies is that few adequately sample a diversity gradient. Some studies compare monocultures to two or three-species mixtures (Augusto *et al.* 2003), whereas others use a dilution gradient, in which one species is present in all stands (Cesarz *et al.* 2007; Sobek *et al.* 2009). Moreover, most work has examined natural forests, which may vary in abiotic conditions. For example, a positive relationship between tree diversity and herb diversity may arise from among-site variation in soil fertility. So far, no study has assessed the effects of tree diversity on understory diversity while controlling for the effects of tree identity and abiotic variables.

In this contribution, we sample the understories of 45 sites, in which the canopy layer is dominated by all possible combinations of four tree species in a managed forest in the Czech Republic. We investigate the effects of tree species diversity, tree identity, and abiotic features on the diversity of three groups of understory organisms that are important for ecosystem functioning: litter-dwelling earthworms, litter-dwelling beetles, and herbs. Using structural equation modelling (Grace 2006), we distinguish the direct effects of trees on the understory from those mediated by abiotic conditions. We hypothesize that: 1) Tree diversity positively affects herb, beetle and earthworm diversity, and that 2) Tree identity and diversity have both direct and indirect effects on understory diversity.

Methods

Location

The Training Forest Enterprise (TFE) is located north of Brno: 49°3'N and 16°7'E, and 210 to 574m above sea level (see Fig. 1 in General Introduction). The annual mean temperature is 7.5°C to 8.1°C, the average annual precipitation is 528 to 685mm, and 360mm during the growing season, and Cambisol is the main soil type (Truhlář 1997). Forest type, age, density, and volumetric species composition are estimated in each stand every ten years and made publically available (www.mapserver-slp.mendelu.cz/).

Sampling design

Forests of the TFE are dominated by an evergreen conifer, *Picea abies* (Norway spruce), a deciduous conifer, *Larix decidua (*European larch), and two broadleaved tree species *Quercus petraea* and *Fagus sylvatica* (Sessile oak and European beech, respectively). Sites dominated by all possible combinations of these four focal species were sampled (see

Table 1 in General Introduction), and replicated three times. Our sampling design thus incorporated 45 forest sites and 15 different species compositions. Sites ranged from 0.07 to 0.6 ha, and were 0.24 ha in average.

Data collection

In every site, six trees of every focal species were targeted, and the positions of targets and their neighbours in a 10-m radius were mapped with the Field-Map technology (http://www.fieldmap.cz/). Every mapped tree was identified, and its diameter at breast height (DBH) measured. For understory sampling, a transect 40 x 20 m was established in every site, along which herbs, beetles, earthworms and abiotic characteristics were assessed.

For Herbs, forty-one 1-m^2 randomly located plots divided into 20 by 20 cm sub-grids (i.e., 25 sub-grids per plot) were established along all transects. In each plot, the relative abundance of each herb species was estimated by counting the number of sub-grids in which the species was present. Sampling 41 plots was sufficient to saturate the species-accumulation curve.

Beetles and earthworms were sampled in 5m-radius plots at the ends and middle of each transect. We collected humus (ground litter and leaf mould) in five randomly selected 30 by 30 cm sub-plots. Humus was sifted using an entomological sifter with a 10-mm wire-mesh screen bottom. Material sifted through the screen was exposed to the sun on a white cloth for about 15 minutes, and beetles were manually collected. Large earthworms were collected prior to sifting, and small ones following sun exposure.

We assessed the abiotic conditions of each site in the following way. To determine the mass of the humus layer, all the humus from the top litter layer to the mineral soil was collected from 100-cm^2 quadrats at nine points along each transect, dried, and weighed. Canopy cover was measured using hemispherical photographs taken with Cannon EOS 550 camera with Sigma circular fish-eye lens at five points along each transect. The hemispherical photographs were analysed using Can-Eye V6.36 software. Finally, soil samples were taken at both ends of all transects, and pH, C/N ratio, and phosphorus content were measured. Herb, humus and canopy cover data were collected between July and August 2012, and beetles and earthworms in June 2012.

The tree neighbourhood maps were used to calculate tree diversity, relative abundance of all focal species, and tree density for every site. Tree diversity was calculated as the effective number of canopy trees, or the exponent of the Shannon index $e^{H'}$, which takes both richness and evenness into account. Tree density and relative abundance were calculated on basal area: tree density was defined as total basal area of canopy trees ($m^2 \cdot ha^{-1}$), and relative abundances were measured as proportions (basal area of species *i* / total basal area of canopy trees).

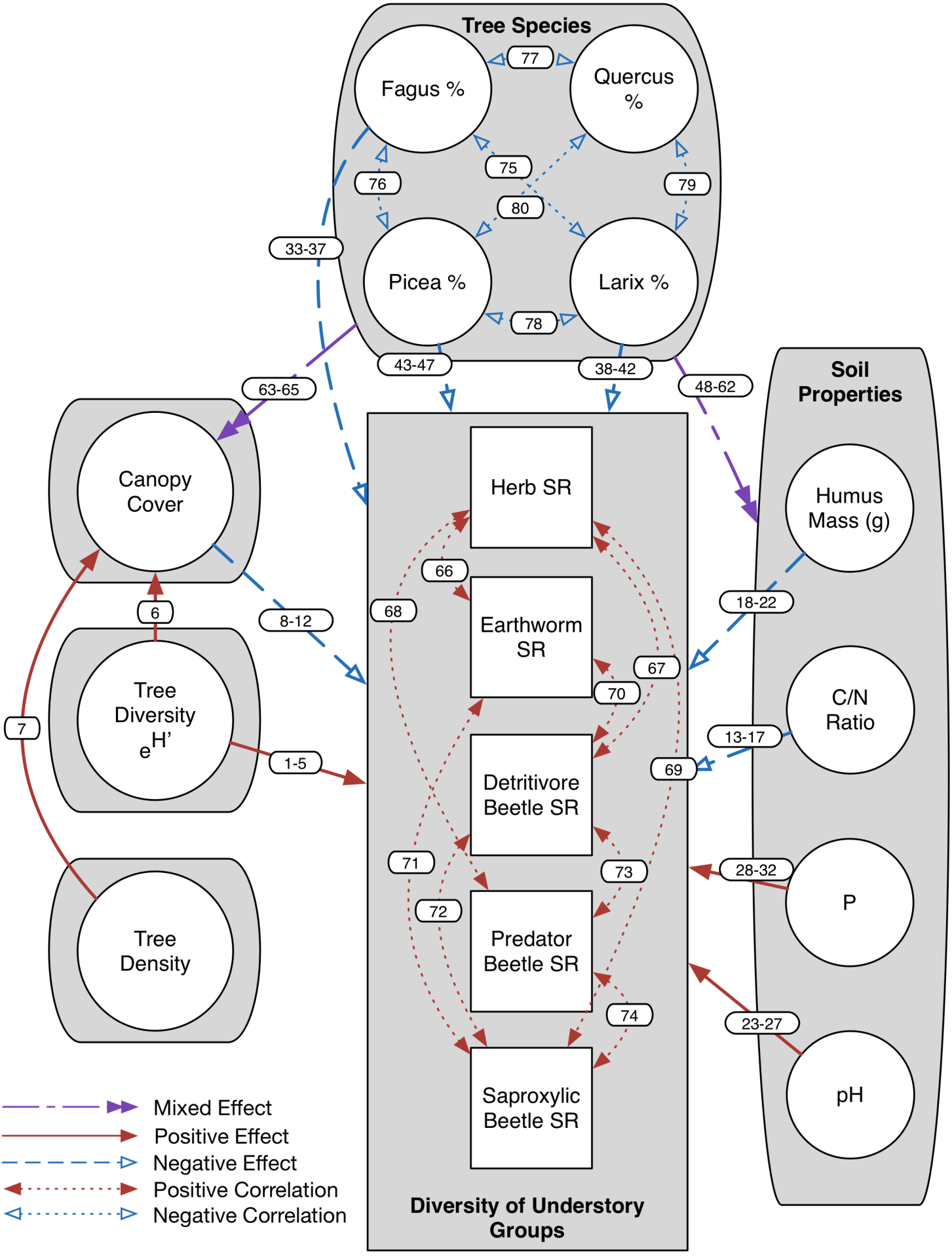
We classified beetles into four groups based on their feeding habits because we expected their responses to the tested variables to differ (Lassau *et al.* 2005). The four functional groups were predators, which feed on other animals (usually invertebrates); herbivores, which feed on live plants; detritivores, which feed on dead organic matter; and saproxylics, which consume dead wood. For herbs, earthworms and each functional group of beetles, gamma diversity was calculated as the total species richness per site. Finally, abiotic measures, including humus mass weight, canopy cover and soil variables were averaged at the site level.

In total, we found 6 earthworm species (mean 2.4 per site, range 0-4), 128 beetle species (mean 8.7, range 3-16) and 181 herb species (mean 26.8, range 1-50). Of the beetle species, 42 species were detritivores (mean 2.8, range 0-11), 37 predators (mean 2.4, range 0-5), 30 herbivores (mean 2.2, range 0-5), and 19 saproxylics (mean 0.9, range 0-4). Because our sampling method could not reliably capture herbivore diversity they were omitted from further analysis.

Statistical analysis

We used structural equation modeling (SEM, Grace 2006) to quantify the direct effects of canopy tree diversity, identity and density on the species richness of earthworms, beetles and herbs and on the beta diversity of herbs, as well as their indirect effects, mediated by abiotic conditions. First, we created a SEM meta-model representing hypothesized relationships. The SEM meta-model is diagrammed in Figure 1, in which paths between variables represented hypothesized correlations and causal relationships.

Figure 1: SEM meta model, showing hypothetical effects (implying causality between two variables) and correlations (no causality) between variables. When an effect is shown with a group of variables, it involves as many effects as there are variables. For example, paths 1-5 from tree diversity to diversity of understory groups mean path 1 to herb SR, path 2 to earthworm SR, path 3 to detritivorous beetle SR, path 4 to predatory beetle SR, and path 5 to saproxylic beetle SR. Mixed effects stand for effects of different signs from one group of variables to the other that were too complex to all include in this diagram. Sharp corner-boxes are response variables, round corner are explanatory. See Figures 2 and 3 for more details of these interactions.


Tree Species
Fagus %
Quercus %
Picea %
Larix %
77
75
76
79
80
78
33-37
43-47
38-42
48-62
63-65
Soil Properties
Humus Mass (g)
C/N Ratio
P
pH
Canopy Cover
Tree Diversity eH'
Tree Density
6
7
8-12
1-5
18-22
13-17
28-32
23-27
Herb SR
Earthworm SR
Detritivore Beetle SR
Predator Beetle SR
Saproxylic Beetle SR
66
68
67
70
69
71
73
72
74
Diversity of Understory Groups
Mixed Effect
Positive Effect
Negative Effect
Positive Correlation
Negative Correlation

We hypothesized that tree diversity would directly promote diversity of all tested taxa (paths 1-5) due to increasing habitat heterogeneity because such relationship was previously reported for herbs (Vockenhuber *et al.* 2011), earthworms (Cesarz *et al.* 2007) and beetles (Sobek *et al.* 2009). We also expected tree diversity and density to increase canopy cover (paths 6 and 7) and canopy cover to decrease herb (Vockenhuber *et al.* 2011) and invertebrate diversity (paths 8-12), because in the forests of TFE, more soil beetle species have been found in sites with open canopy structure than in closed forests (Stejskal, unpublished data). Of the soil variables, C/N ratio and humus mass are usually negatively correlated with nutrient availability, and, therefore, they both are likely to negatively affect diversity of herbs and of soil invertebrates (C/N ratio: paths 13-17, humus mass: 18-22). On the other hand, soils with higher pH and P were found to support higher diversity of herbs (Augusto *et al.* 2003) and earthworms (Cesarz *et al.* 2007) and thus we also expected them to also support higher diversity of all tested functional groups of soil beetles (pH: paths 23-27, P: paths 28-32).

Of the tree species, we hypothesized that relative abundance of *Fagus*, *Picea* and *Larix* would have direct negative effects on diversity of all tested taxa (paths 33-37, 38-42, and 43-47 for *Fagus, Larix,* and *Picea,* respectively Fig. 1) because stands dominated by conifers or *Fagus sylvatica* often have lower understory diversity in temperate Central European forests (Cesarz *et al.* 2007; Barbier *et al.* 2008; Sobek *et al.* 2009). In addition, *Fagus*, *Picea* and *Larix* produce slow-decomposing litter. Thus we predicted that increasing relative abundance of these species would increase litter amount (paths 48-50 for *Fagus, Larix,* and Picea, Fig. 1, 2 and 3) and C/N (paths 51-53, Fig. 1, 2 and 3) and decrease P content (paths 54-56, Fig. 1, 2 and 3) in soils. Because conifers produce litter of low pH compared to hardwoods (Augusto *et al.* 2003), we also hypothesized that increasing relative abundances of *Larix* and *Picea* would

decrease soil pH (paths 57 and 58 for *Larix,* and *Picea*, Fig. 1 and 2), whereas we expected *Quercus* to be positively correlated with pH (path 59, Fig. 1 and 3), based on our field observation. Besides, we expected that increasing relative abundance of *Quercus* would lead to a decrease in litter weight (path 60, Fig. 1 and 3) and C/N (path 61, Fig. 1 and 3) as well as an increase in P content (path 62, Fig. 1 and 3) due to fast decomposition rates and higher nutrient content of its litter (Hobbie *et al.* 2006). In our meta-model, increasing relative abundance of *Quercus* would cause a decrease in canopy cover (path 63, Fig. 1 and 3) due to its shade intolerance, and relative abundance of *Fagus* and *Picea* would on the contrary increase canopy cover (paths 64 and 65, Fig. 1, 2 and 3).

Additionally we supposed that herb diversity would be positively correlated with the diversity of all invertebrate taxa (paths 66-69, Fig. 1) due to increased litter and habitat diversity. We expected that diversities of earthworm, detritivore and saproxylic species would be positively correlated (paths 70-72, Fig. 1) due to similar responses to tested explanatory variables, and that the diversity of predator beetle species would positively correlate with diversity of other beetle taxa (paths 73 and 74, Fig. 1) because higher diversity of these represents higher food diversity for the predators. Finally, we expected that all pairs of tree species abundances would be negatively correlated, because an increase in the proportion in one species would naturally mean a decrease in the proportion of (paths 75-80, Fig. 1, 2, and 3).

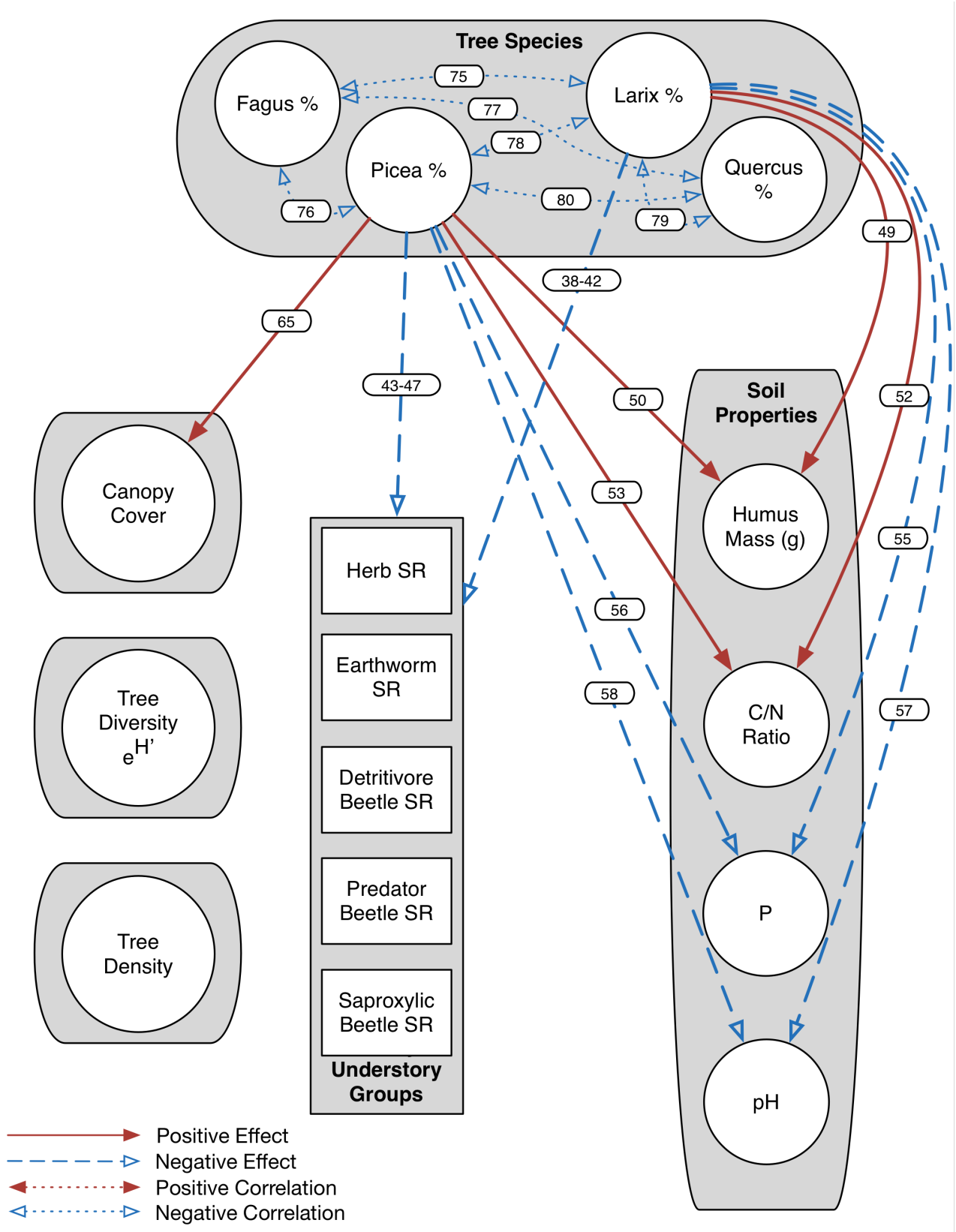


Figure 2: Effects of the relative abundances of *Larix* and *Picea* on biotic and abiotic components of the SEM. It shows hypothetical effects (implying causality between two variables) and correlations (no causality) between variables. When an effect is shown with a group of variables, it involves as many effects as there are variables. For example, paths 43 to 47 show the expected effects from *Picea* to the diversity of herbs, earthworms, detritivores, predators, and saproxylics.

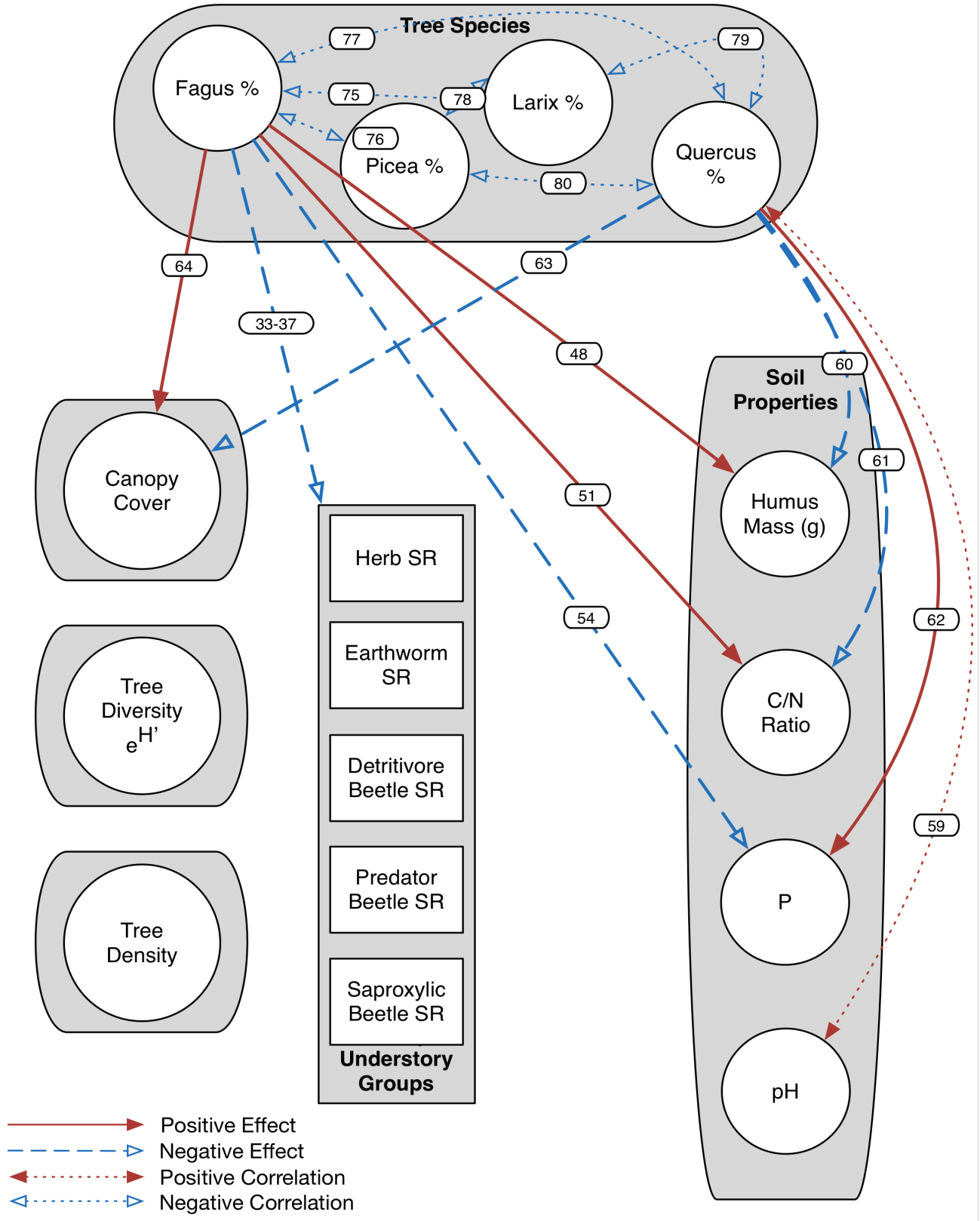


Figure 3: Effects of the relative abundances of *Fagus* and *Quercus* on biotic and abiotic components of the SEM. It shows hypothetical effects (implying causality between two variables) and correlations (no causality) between variables. When an effect is shown with a group of variables, it involves as many effects as there are variables. For example, paths 33 to 37 show the expected effects from *Fagus* to the diversity of herbs, earthworms, detritivores, predators, and saproxylics.

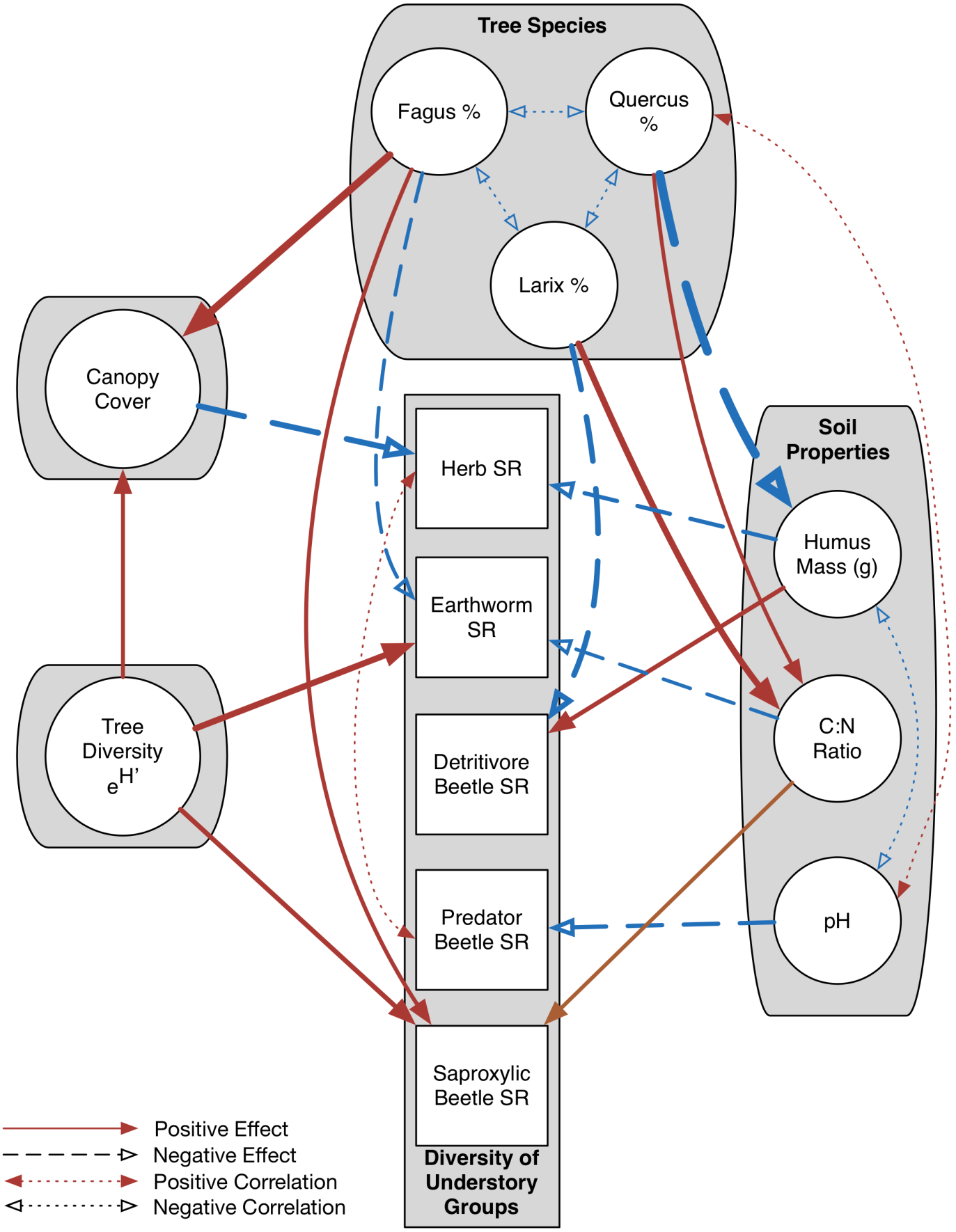


Figure 4: Results from the selected SEM showing the significant effects and correlations between variables. The width of the effect arrows is proportional to the standardized coefficients. See Figures 5 to 9 for the detailed values.

Based on the meta-model, we specified an initial SEM model in which all possible paths (within the meta-model specifications) were included. Standardized regression coefficients (SC), standard errors and P-values were calculated for every path using the maximum likelihood estimation method. The initial SEM model was simplified by removing non-significant paths ($P > 0.05$). The model fit was tested using Chi-square as well as Root Mean Square Error of Approximation (RMSEA) and 90% RMSEA Confidence Intervals. In the final model, we calculated regression coefficients, standard errors and P-values for indirect effects. The procedure of SEM model creation, selection and testing followed Grace (2006) and Grace *et al.* (2012) and was performed with the lavaan package (Rosseel 2012) in the R 2.12.0 statistical environment (R Development Core Team 2011).

Results

Final model

The final SEM model proved to be significant (Chi-square = 51.81, P = 0.520, 90% RMSEA Confidence Intervals = 0.00 and 0.091; Fig. 4, S1, and S2). Out of all variables in the meta-model, tree density, relative abundance of *Picea* and P content had no significant effect on understory diversity either directly or indirectly.

Herbs

Increasing canopy cover and humus mass reduced the species richness of the herb layer (SC: -0.436 and -0.354, respectively, Fig. 4 and 5). Herb species richness was further reduced by an indirect effect of increasing *Fagus* abundance (SC: -0.272), because it increased canopy cover (SC: 0.598).

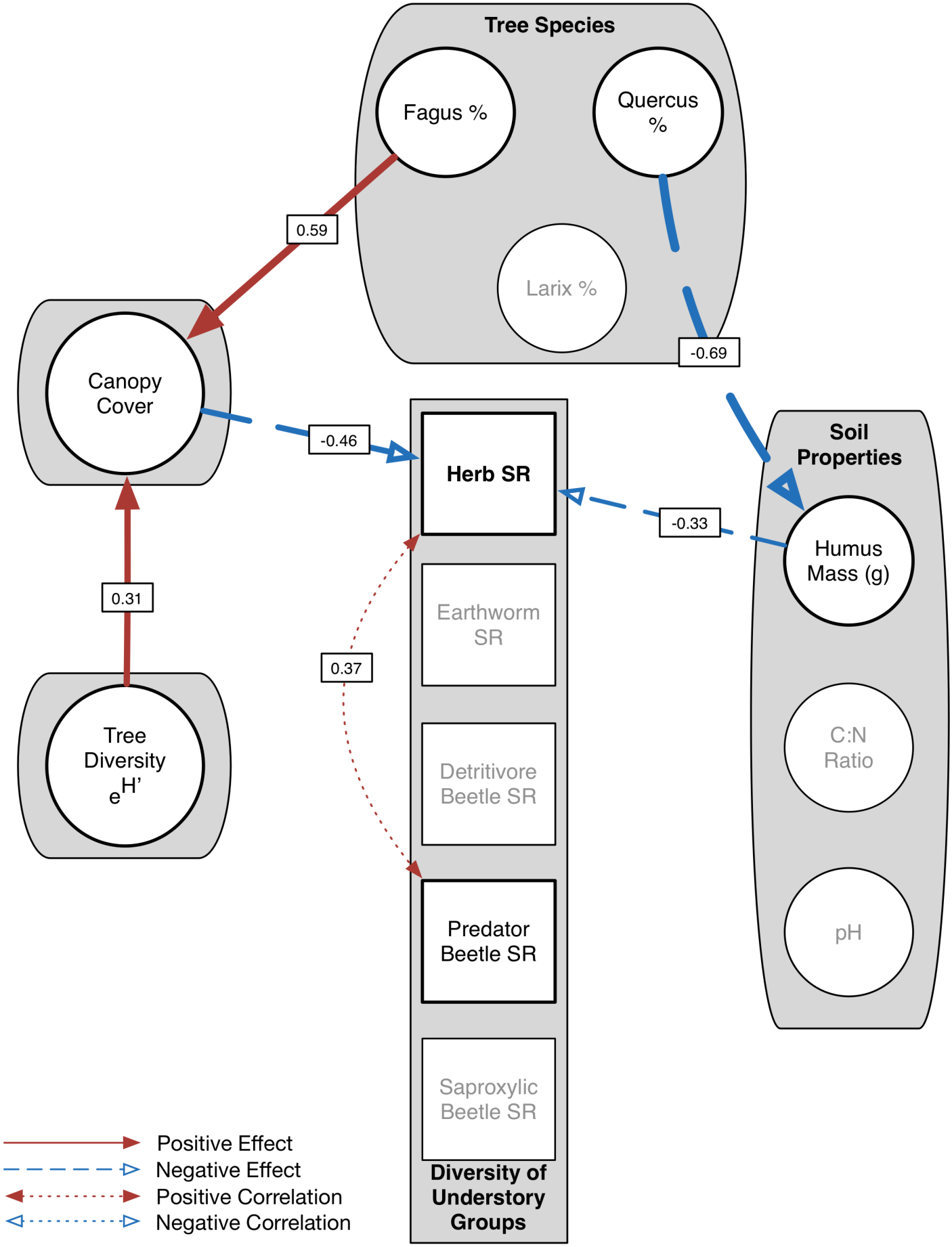


Figure 5: Details of the significant effects on the Species Richness of herbs.

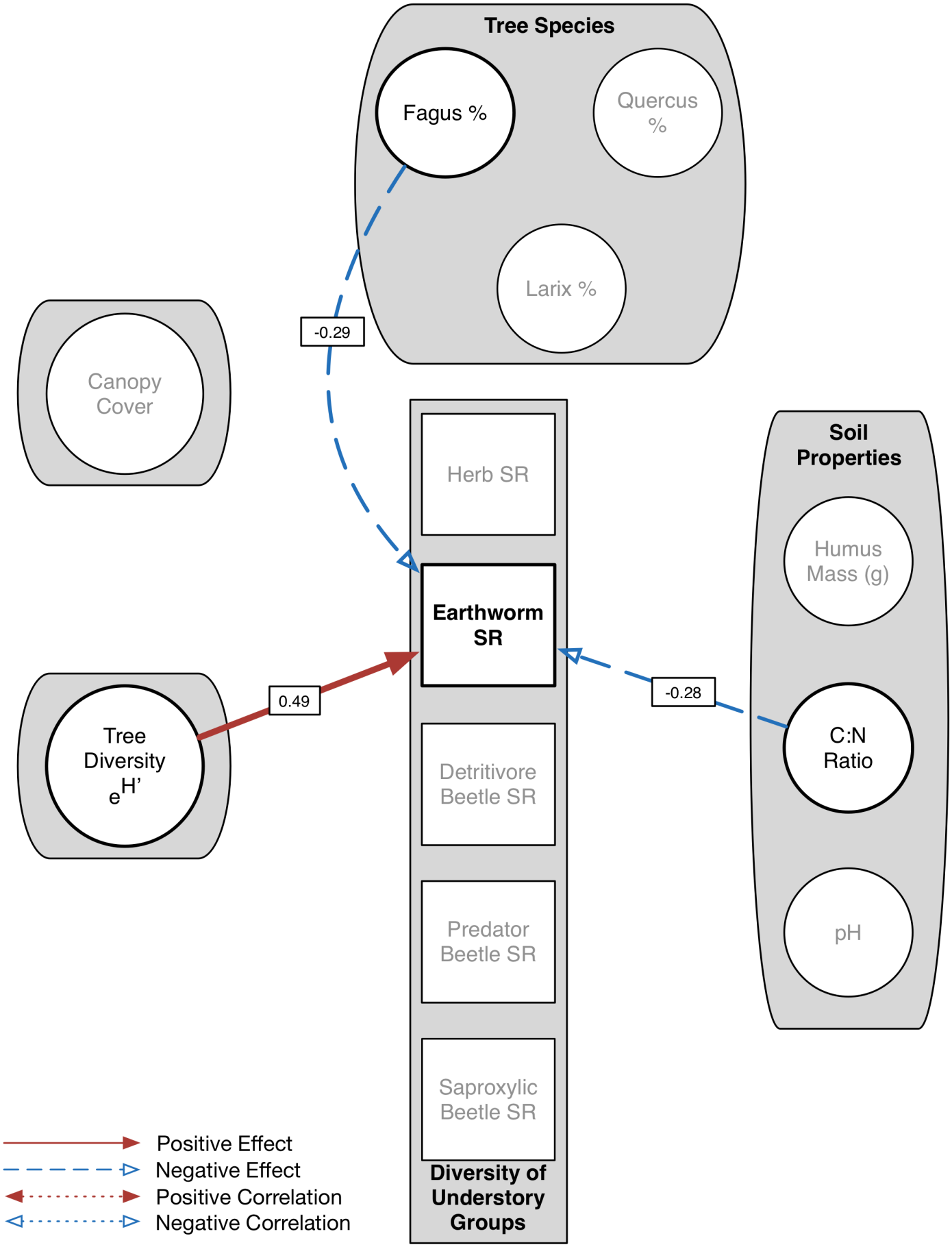


Figure 6: Details of the significant effects on the Species Richness of earthworms.

Quercus abundance also had an indirect effect on herb species richness (SC: 0.229), which was mediated by its negative effect on humus mass (SC: -0.686). Contrary to expectations, tree diversity had an indirect effect on herb species richness (SC: -0.134) mediated by its positive effect on canopy cover (SC: 0.306).

Earthworms

Earthworm diversity was directly affected by tree species diversity, the relative abundance of *Fagus,* and C/N ratio (Fig. 4 and 6). Of these paths, the positive effect of tree diversity was the strongest, with a standardized regression coefficient (SC) of 0.486. Increasing *Fagus* abundance and C/N ratio reduced earthworm diversity (SCs: -0.287 and -0.282, respectively). No significant indirect effects were detected.

Beetles

Saproxylic beetle diversity increased most strongly with increasing tree diversity (SC: 0.382, Fig. 4 and 7), but was also positively affected by C/N ratio and the abundance of *Fagus* (SC: 0.315 and SC: 0.307, respectively). In addition, increasing *Larix* abundance increased C/N ratio (SC: 0.493), and thus indirectly boosted saproxylic beetle diversity (SC: 0.155).

Increases in humus mass and reductions in *Larix* abundance increased the diversity of detritivore beetles (SC: -0.440 and 0.343, respectively, Fig. 4 and 8). Increasing *Quercus* abundance reduced humus mass (SC: -0.686), and thus had a negative indirect effect on detritivore diversity (SC: -0.235). The diversity of predatory beetles was negatively affected by pH (SC: -0.339, Fig. 4 and 9) and positively correlated with herb species richness ($r = 0.372$, $P = 0.020$).

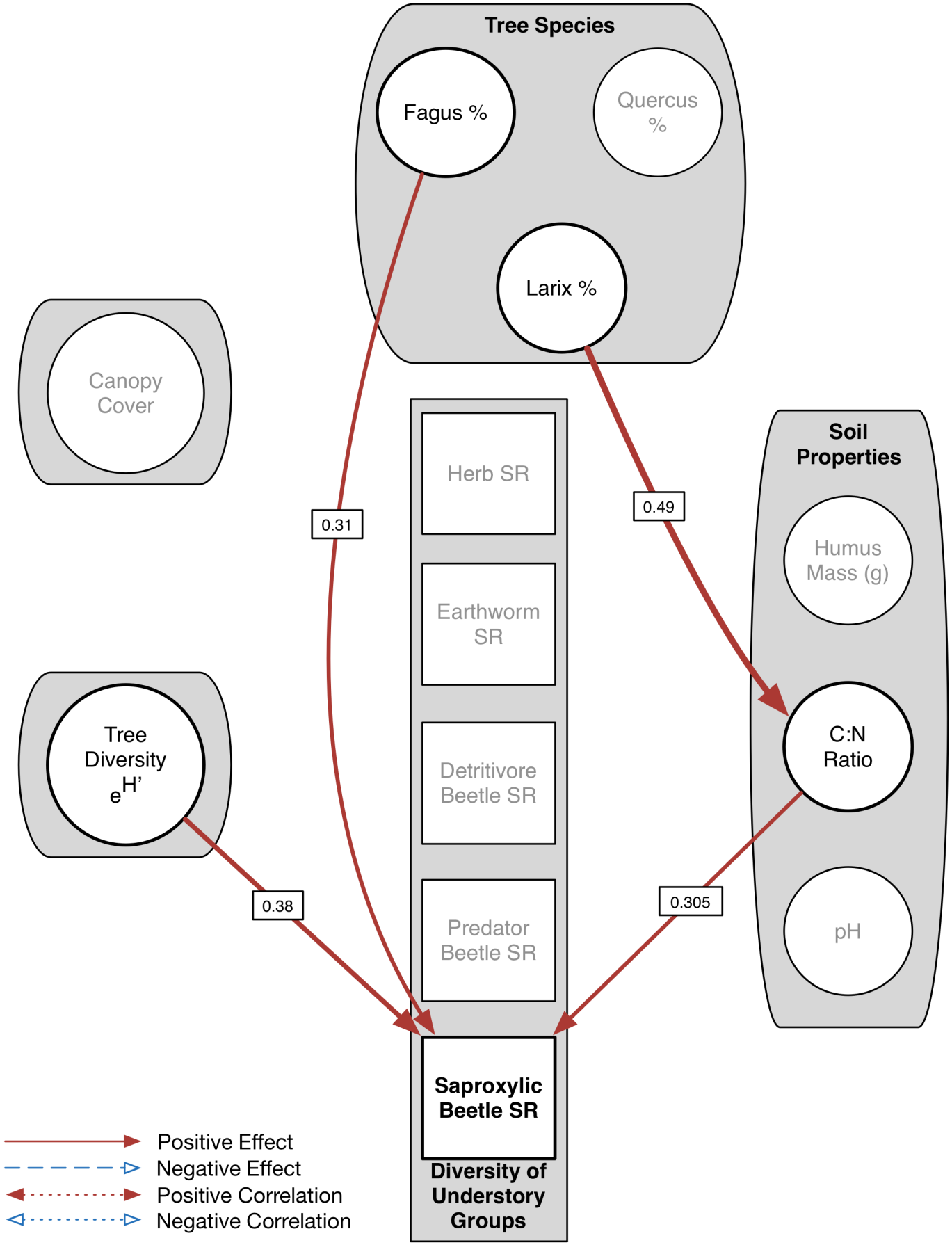


Figure 7: Details of the significant effects on the Species Richness of saproxylic beetles.

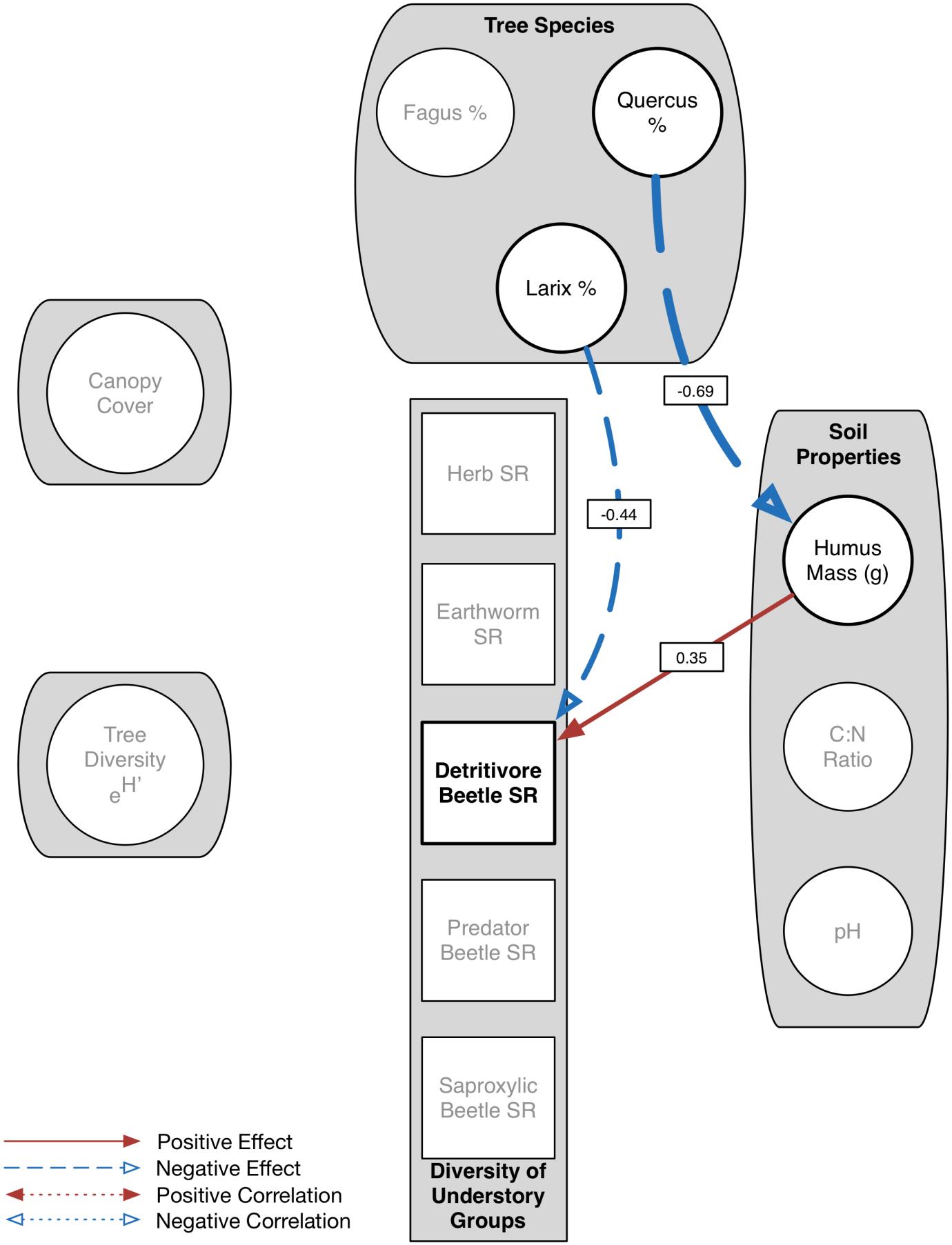


Figure 8: Details of the significant effects on the Species Richness of detritivorous beetles.

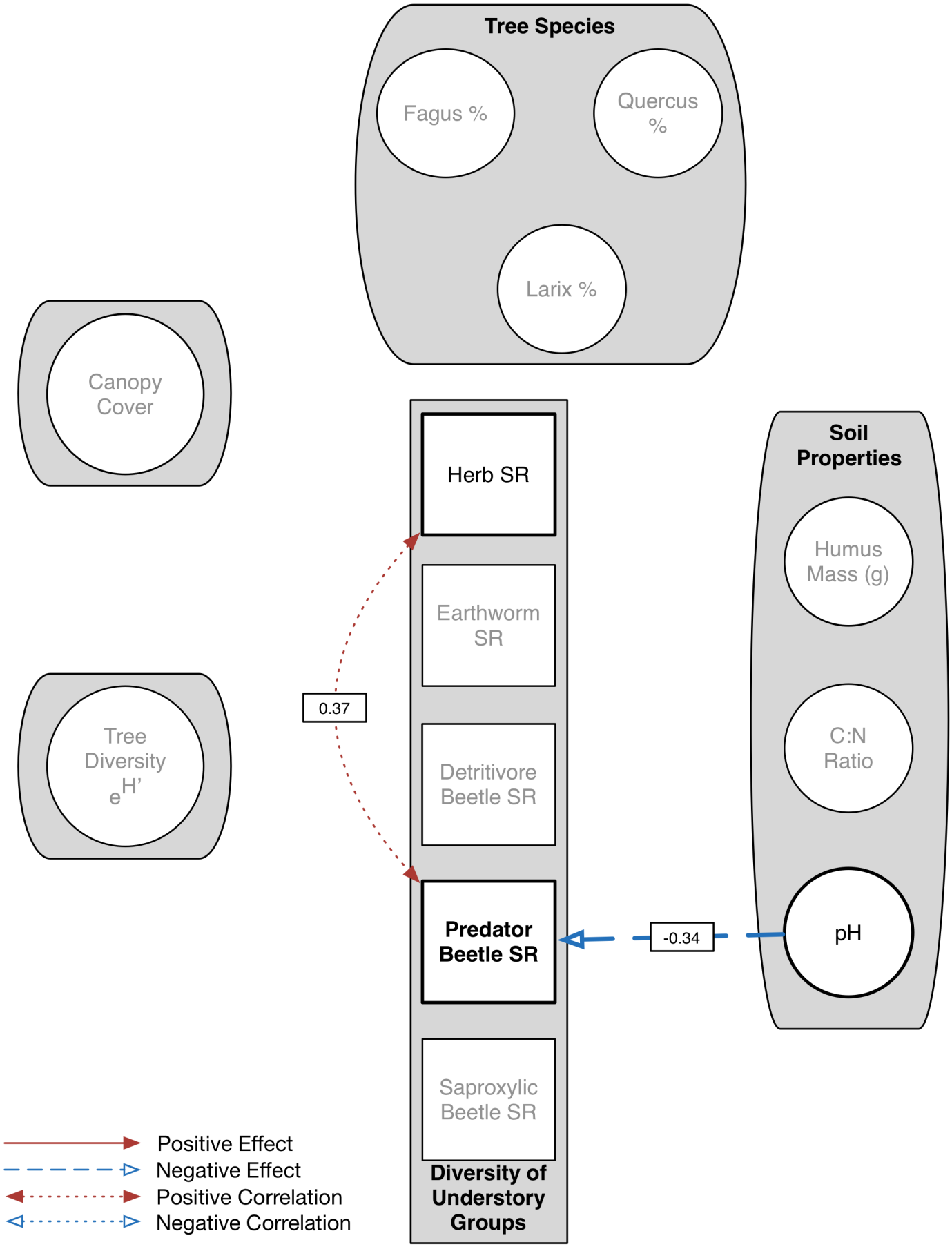


Figure 9: Details of the significant effects on the Species Richness of predatory beetles.

We also found negative correlations between all pairs of the relative abundances of *Fagus, Larix*, and *Quercus,* and between pH and humus weight, as well as a positive correlation between pH and the abundance of *Quercus* (Fig. 4-9).

Discussion

Our study showed that tree diversity promotes the species richness of earthworms and saproxylic beetles, two important groups of decomposers, while negatively affecting herb diversity. Previously, tree diversity was found to have either positive or neutral effects on other groups of forest organisms (Nadrowski *et al.* 2010).

The negative effect of tree diversity on herb diversity is not direct, however, but mediated by an increase in canopy cover (Fig. 4 and 9). Increasing canopy cover reduces light penetration to the understory, which is one of the most limiting factors for herb growth (Kirby K J 1988; Jennings *et al.* 1999; Barbier *et al.* 2008). Forest stands with high tree species diversity have greater canopy structural complexity, which allows them a better use of resources, especially light (Morin *et al.* 2011). Because understory herbs need the same resources as trees but cannot outcompete them, the increasing diversity of trees implies a greater pre-emption of these resources by trees, thus leaving less for herbs, leading to a decrease in their diversity. Nevertheless, all previous studies have found positive or neutral effects of tree diversity on herb diversity (Ingerpuu *et al.* 2003; Mölder *et al.* 2008; Nadrowski *et al.* 2010; Vockenhuber *et al.* 2011). They were carried out, however, in natural or semi-natural forests, potentially confounding the effects of tree diversity on herb diversity with abiotic conditions that favoured both tree and herb diversity (Vockenhuber *et al.* 2011). Gilliam (2007) showed a positive relationship between canopy and herb-layer diversity in North American forests, which he explained by a

similar response of both vegetation stratas to environmental gradients. Herb diversity in our study was negatively affected by humus mass, which corroborates other research from temperate forests (Augusto *et al.* 2003; Gazol & Ibáñez 2009; Vockenhuber *et al.* 2011). The humus layer represents a physical barrier for plants to germinate and emerge (Sydes & Grime 1981). The thicker it is, the fewer species can grow through it (Dzwonko & Gawroński 2002).

Of tree identity, beech had a negative effect on herb diversity mediated through an increase in canopy cover, while oak had a positive effect mediated through a decrease in humus mass. Similarly, some studies found beech to significantly decrease herb species diversity (Mölder *et al.* 2008). Beech is by far the most shade-tolerant tree species in our forests, and may grow under the canopy of other light-demanding species. Thus, increasing its abundance leads to an increase in canopy cover. Due to its dense fine root network (Leuschner *et al.* 2004), it is also a strong competitor for water and nutrients, and thus may limit growth of many understory herbs (Falkengren-Grerup & Tyler 1993). Oak produces a quickly decomposing litter (Hobbie *et al.* 2006), and forms light humus compared to the other tree species.

We found that tree diversity had large, positive, and direct effects on the diversity of earthworms and saproxylic beetles. The positive effect of tree diversity on earthworms in natural forest was also found by Cesarz *et al.* (2007), who explained it by an increased diversity in food quality, due to increasing litter diversity. Species richness of saproxylic beetles has been found to be positively correlated with dead wood diversity (Similä, Kouki & Martikainen 2003), which in turn is likely to be correlated with tree species diversity. Surprisingly, we found no relationship between the diversity of trees and detritivores. As trees are the main producers of leaf litter, we expected that tree diversity should foster a diverse detritivore

community. This lack of effect could have arisen if detritivorous beetles are generalist consumers and therefore not as responsive to litter composition and diversity as saproxylic beetles or earthworms. Interestingly, our results showed that the diversity of predatory beetles was positively correlated with herb diversity but not with tree diversity. Hättenschwiler, Tiunov & Scheu (2005) suggested that more diverse plant communities support considerably higher predator densities due to higher plant-litter diversity. This is likely to be the mechanism behind the positive correlation between predator beetles diversity and plant diversity in our study, but, unlike earthworms and saproxylic beetles, the herb layer diversity is the driver of the effect, not the tree diversity.

As expected, soil variables significantly affected understory diversity. Increasing C/N ratio reduced earthworm diversity but increased saproxylic beetle diversity. C/N ratio is negatively correlated with litter quality, which is crucial for the composition, performance and growth of decomposers, and thus is likely to have negative impact on earthworm diversity (Hättenschwiler *et al.* 2005; Milcu *et al.* 2006). The mechanism linking C/N ratio to saproxylic beetle diversity is less obvious. Several studies have found a positive correlation between saproxylic beetle diversity and the availability of dead wood (e.g. Økland *et al.* 1996; Martikainen *et al.* 2000; Similä *et al.* 2003). A higher C/N ratio usually implies slower litter decomposition rates (Enriquez, Duarte & Sand-Jensen 1993) including the decomposition of dead wood in the litter layer, which is then more likely to remain in higher quantities and for longer time in the understory, supporting a higher diversity of this functional group of beetles. Humus mass had a positive effect on the diversity of detritivores, which makes sense since humus contains the detritus on which this group feeds. But also, more humus implies a more stable environment for these beetles because it is less likely that the humus layer completely decomposes at some point of the year. pH was previously found to positively affect the diversity of herbs (Härdtle, von Oheimb & Westphal

2003; Vockenhuber *et al.* 2011) and earthworms (Cesarz *et al.* 2007), but this effect did not appear in our analysis. However, oak's relative abundance, which had an indirect and positive effect on herb species richness, was positively correlated with pH.

Beech, oak and larch had a variety of effects on understory diversity, whereas spruce affected none of the studied groups of organisms. Increasing the relative abundance of beech had a significant negative effect on earthworm diversity, but a positive effect on the diversity of saproxylic beetles. Beech litter has the slowest decomposition rate of the four studied tree species (Hobbie *et al.* 2006), so that it is likely less favourable for decomposers such as earthworms. But because it decomposes slowly, and perhaps also because of its chemical composition, beech's dead wood favours the diversity of saproxylic beetles more than other studied tree species. The relative abundance of larch had a positive and indirect effect on the diversity of saproxylic beetles, mediated through an increase in C/N ratio. Increasing relative abundance of larch significantly decreased the diversity of detritivore beetles which is likely due to less favourable litter properties, with higher N – immobilisation and lower content of key nutrients such as Ca and K in comparison with oak, beech and spruce (Hobbie *et al.* 2006).

Conclusion

Our study showed that contrary to previous work, tree diversity reduced herb diversity, because diverse communities of trees reduce the availability of resources for understory herbs. This could negatively affect some functions of the herb layer like biomass production (Yarie 1980), but is likely to be buffered by the positive effect of tree diversity on wood production (Nadrowski *et al.* 2010, Chapter 2). Moreover, we found tree diversity to directly enhance the diversity of earthworms and saproxylic

beetles, two important groups of decomposers. Both participate in nutrient cycling (Hättenschwiler *et al.* 2005; Cobb *et al.* 2010), and affect the composition and activity of soil biota (Scheu *et al.* 2002), which in turn supports the structure and functioning of the aboveground community including plant growth and productivity (Wardle *et al.* 2004).

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Supplementary material

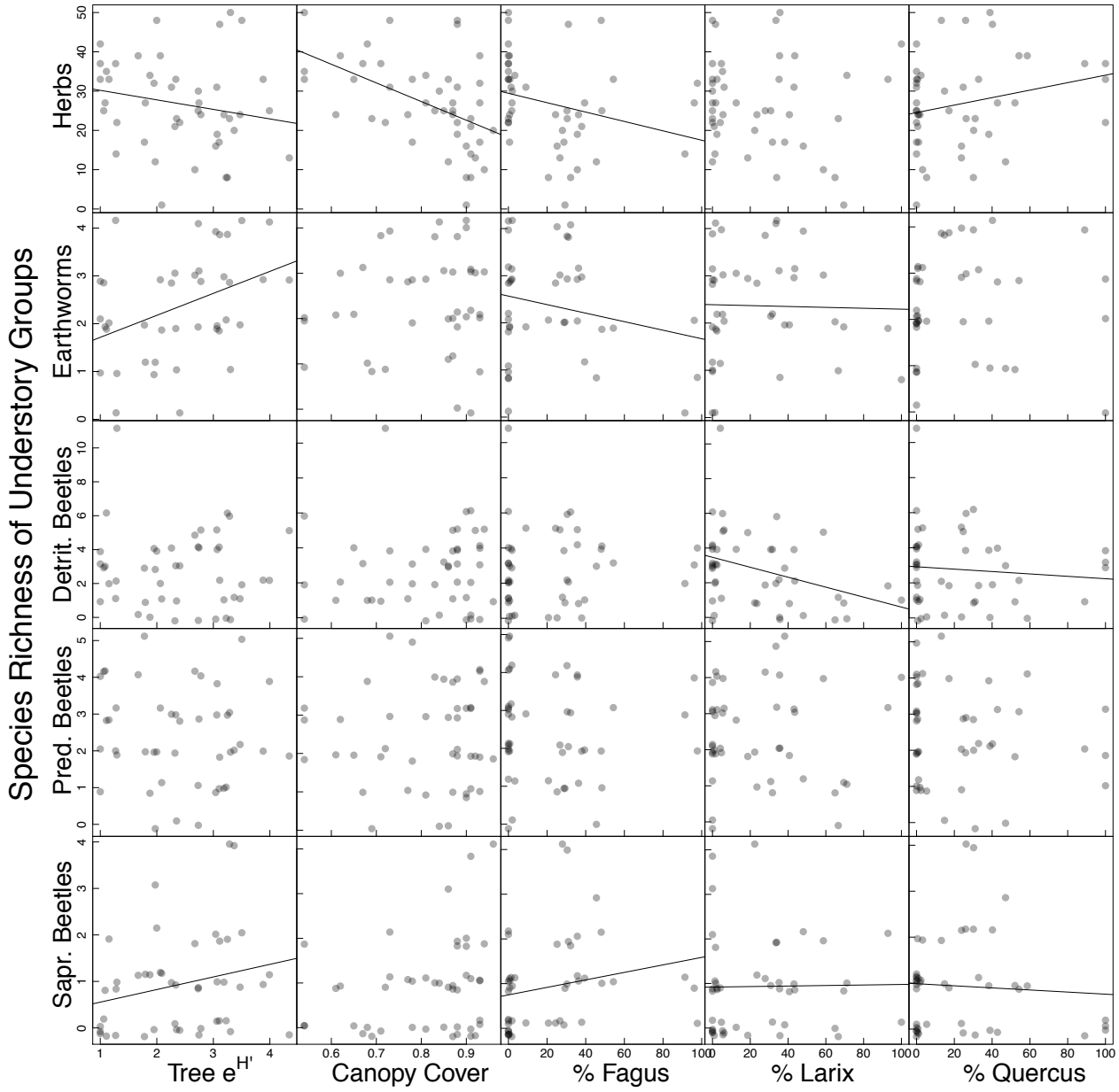

Figure S1: Scatterplots of all response variables jittered on the y-axis, against all explanatory variables that are related to the tree layer on the x-axis. The fit of a linear model is shown for direct and indirect paths that were significant in the final SEM.

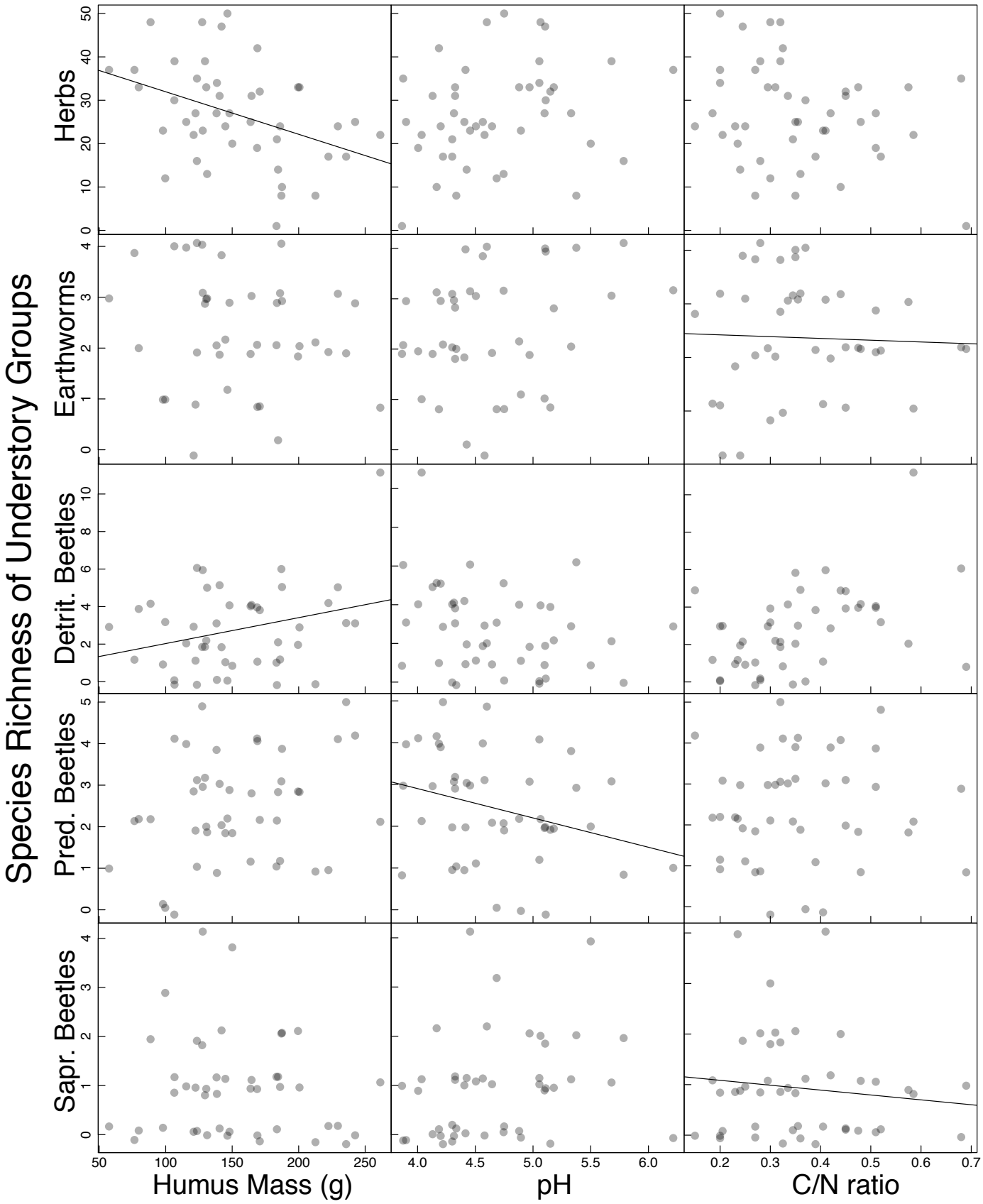

Figure S2: Scatterplots of all response variables jittered on the y-axis, against all explanatory variables that are related to the soil on the x-axis. The fit of a linear model is shown for direct and indirect paths that were significant in the final SEM.

General Discussion

In this thesis I examine the effects of tree species diversity on two properties of forests: their functioning and stability. I take a multi-disciplinary approach to this topic combining dendrochronological methods, spatial mapping technology, diversity census of several groups of organisms, and various analytical methods.

Biodiversity and ecosystem functioning

Using the information contained in tree rings, we were able to explore individual tree growth, and found that it increased with species diversity (Chapter 2). This effect was independent of tree density, showing that the growth of individual trees directly benefit from diversity, in this managed forest. Our sampling design didn't allow us to estimate productivity at the site level because we were not able to core every tree in a neighbourhood or stand. For the same reasons, we could not explore the relative contributions of the complementarity and selection effects to the net effect of diversity. However, we showed that the effect of diversity on growth of different species in mixtures was independent of species identity, which is an indication that complementarity might be at play since all species appeared to benefit. Using structural equation modelling, we disentangled the effects of species diversity from those of species identity on the understory (Chapter 4). We found a positive and direct effect of species diversity on the diversity of earthworms and saproxylic beetles, two important groups of litter decomposers. Tree diversity thus simultaneously affects different forest functions.

The effect of species diversity on ecosystem multifunctionality has received a growing interest over the past decade (Hillebrand & Matthiessen 2009; Isbell *et al.* 2011), and several approaches have been used to calculate multifunctionality (Hector & Bagchi 2007; Zavaleta *et al.* 2010; Maestre *et al.* 2012; Gamfeldt *et al.* 2013). Here I used a simple method proposed in Maestre et al., (2012) and calculated the standardized deviates (Z-scores) of the three functions considered (tree growth, earthworm and saproxylic beetle species richness) to quantify multifunctionality. The multifunctionality index, obtained from averaging over z-scores, measures all functions on a common scale, where all have a mean of zero and a standard deviation of one (Maestre *et al.* 2012). I fitted a linear regression against species diversity (the effective number of species $e^{H'}$), and found the multifunctionality index to increase by 0.34 [95% CI: 0.28-0.41] for every additional species (Fig. 1).

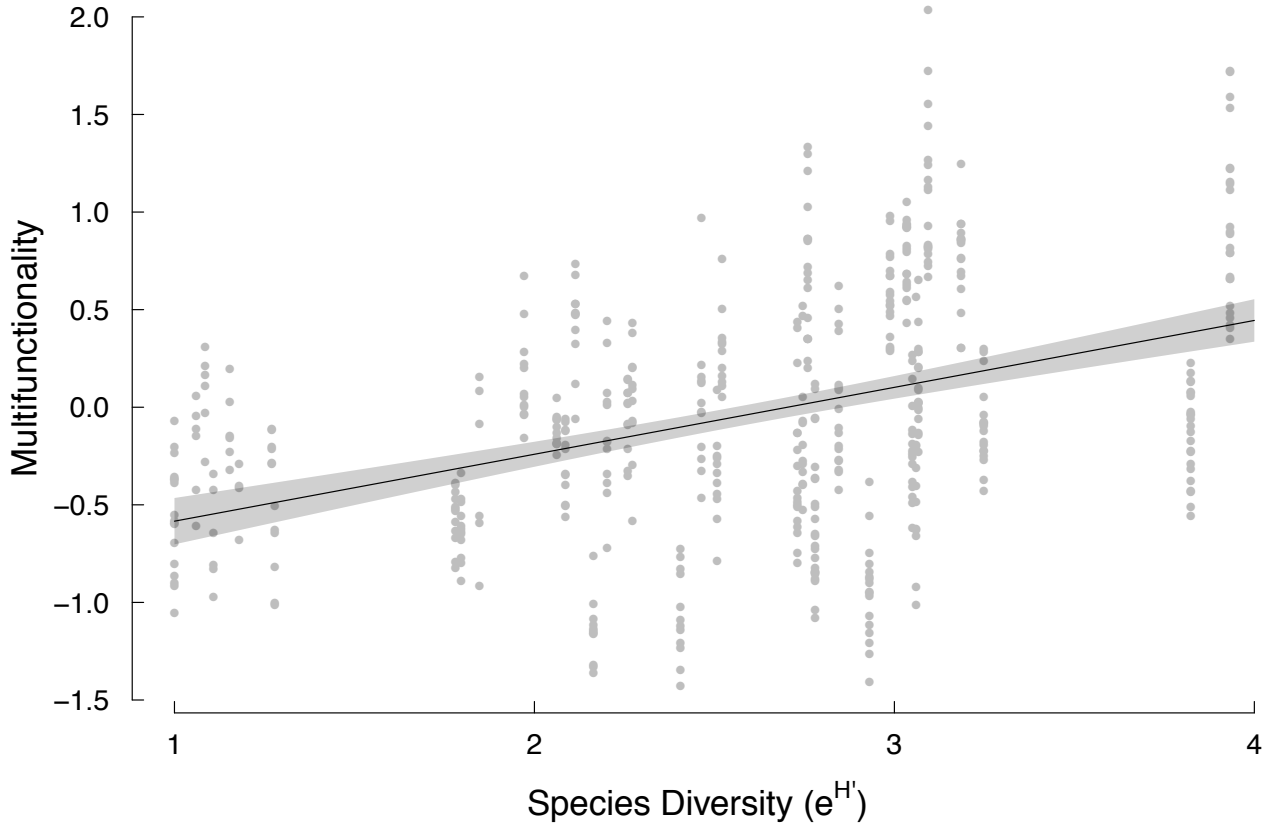

Figure 1: Best-fitting linear regression model of multifunctionality against species diversity ($R^2 = 0.17$, $P < 0.001$). The grey dots show the original data, and the black line and grey-shaded area show the predictions from the model (mean and 95% CI, respectively).

Biodiversity and ecosystem stability

Ecosystems undergo fluctuations in their biotic and abiotic environment, and these fluctuations affect their dynamics and functioning (Cardinale *et al.* 2012). Under rapidly changing conditions induced by human activities, it is crucial to understand how the stability of ecosystems can be maintained (Rockström *et al.* 2009; Cardinale *et al.* 2012). A common way to quantify variability in ecosystem functioning, is to use the coefficient of variation (CV), a dimensionless index that indicates greater temporal stability at lower values e.g. (Hector *et al.* 2010). Experiments conducted in grasslands showed that species richness increased the CV of populations and decreased that of communities (Hector *et al.* 2010; Loreau & de Mazancourt 2013). The authors explained that asynchronous fluctuations of different species over time buffer the net primary production of the whole system (Yachi & Loreau 1999; Lehman & Tilman 2000). In a recent review on the topic, Loreau & de Mazancourt (2013) argued that the three mechanisms by which diversity increases ecosystem stability are asynchrony between species, differences at which they respond to perturbations, and reduction in the strength of competition. Because it is not possible to differentiate between individual grasses, the effect of species diversity on the temporal variation of individuals was not tested. Although individual trees are easily differentiated in forests, they have been much less investigated, and most work on stability focuses on tree response to climate (Babst *et al.* 2013) or biotic disturbances such as pest outbreaks (Jactel, H Brockerhoff, E Duelli 2005). A very recent and inspiring study used tree rings to look at growth compensations between species, following biotic disturbances in mixed forests (Perot, Vallet & Archaux 2013). They showed that tree ring series of oaks and pines were usually synchronous and positively correlated due to common climatic forcing, but that after a pest outbreak that had defoliated pines, their growth trajectories were negatively correlated. Pines suffered a reduction in growth in the four years following the pest outbreak, which was

compensated at the site level by an increased growth for oaks. This is a direct indication that in mixtures, competing species are complementary in their resource use, and following such biotic disturbances, growth compensations allow the stand productivity to be more stable through time.

Here using tree ring series, we showed that the temporal variation of individual tree growth was unaffected by the species diversity of stand they grew in (Chapter 2). However, we found a stabilizing effect of stand level tree density on inter annual variation in individual growth, and hypothesized that at higher densities, the directional effect of climatic fluctuations on radial growth was weaker. Using dendrochronological analytic methods, we showed that tree growth was more limited by precipitation in the growing season (especially in May to July) than by temperature (Chapter 3). We also found that species were differently affected by temperature and precipitation, indicating that their differences in physiology or phenology confers them different sensitivities to climate. The strength of the correlation between standardized ring width and climate was not affected by the species richness of the neighbourhoods of the target trees from which tree ring cores were taken. However, our analysis did not allow us to inspect the effect of site level diversity that would account for species richness and evenness (i.e. $e^{H'}$, the effective species richness reflecting both species richness and evenness). Besides, we could not explore the effect of density on climatic response, although competition was found to affect trees' response to climate (Cescatti & Piutti 1998). It would be interesting to look at particularly bad climate years when extreme drought occurred for example, and see if we could detect growth compensations in mixtures. In their work, Perot *et al.* (2013) suggested that growth compensations were more likely to occur following biotic disturbances, maybe because they are much more species specific and thus asymmetrical, than abiotic ones. Indeed, while we did

find differences in the responses to climate of the species studied here all four were mostly limited by low precipitations in the growing season, suggesting that their responses to climate might not be different enough for them show such strong growth compensations. Yet any asynchrony to environmental fluctuations are stabilizing (Loreau & de Mazancourt 2008, 2013), but this stabilizing effect would be visible at the community level, which we haven't measured.

However stability, as calculated by the coefficient of variation, encompasses several ecosystem properties, among which resistance and resilience are particularly useful (Loreau 2010). Resistance describes the ability of an ecosystem to maintain its state when confronted to external perturbations (Harrison 1979; Loreau 2010), and resilience usually stands for "the speed at which a system returns to its original state after a perturbation" (Holling 1973; Loreau 2010). Some research uses the terminology differently, for example Sterk *et al.* (2013) define resilience as the general ability of an ecosystem to maintain its functioning in a fluctuating environment. They divide resilience into two separate phases: resistance, or "the amplitude of disturbance that can be absorbed by the ecosystem without a change in functioning", and recovery, the "speed of return to the original function". In this work they associated resistance with some response traits (e.g. specific leaf area, canopy height etc), and recovery with effect traits such as clonal growth or seed longevity (Sterk *et al.* 2013). Although the relationship between ecosystem complexity and stability has been debated since the 1950's (Loreau 2010), much work is still needed to improve this theoretical and modeling framework, and investigate the effects of biodiversity on ecosystem, population, and individual stability in a fluctuating environment.

Implications for forest management

Even if no effect of species diversity was found on the wood extracted per hectare and per year (Chapter 1), this measure reflects management practices in the past five years only, and not stand productivity. Besides the positive effect of diversity that we found on individual tree growth (Chapter 2) is of great importance for forest management. Industrial roundwood, the part of wood that serves construction and processed timber products, represents 90% of wood removals. Europe is still one of the largest producers of roundwood, with more than 578 million cubic meters produced in 2010 and increasing value of marketed roundwood. This value depends on wood quality, and big trees are needed for construction for instance. In chapter 2, we showed that individual tree growth was increased by 18 to 28% when diversity was increased from one to four species, indicating that biodiversity can be beneficial for forests' economic value. In this thesis, we didn't detect a stabilizing effect of diversity, but previous work on pure conifer stands showed them to be more prone to disturbances such as pest outbreak or wind damage (Jactel, H Brockerhoff, E Duelli 2005). From a forest management point of view, Knoke *et al.* (2007) suggested that maintaining diverse forests was not more expensive than maintaining pure stands, when economic models accounted for the financial risks associated with losses due to disturbances in pure stands.

By exploring the age distribution of trees growing in stands of increasing species diversity, we showed that young forest stands were more species rich (Chapter 1), indicating an evolution of forestry practices over the past century. In his guide to the TFE, Truhlář (1997) describes the evolution of forest management, and explains that foresters used to favor fast growing conifers a hundred years ago and mostly planted them in pure stands, these practices have now moved towards admixing conifers

and broadleaved species. Especially conifer stands now must include at least 5% of deciduous trees in volume in this forest (Truhlář 1997), because pure conifer stands are much more prone to pest outbreaks and wind damage (Truhlář 1997; Jactel, H Brockerhoff, E Duelli 2005). Some monocultures however, are worth sustaining for biodiversity-related reasons. *Quercus petraea* is mostly grown in coppices, where different-aged coppices provide a rich variety of habitats, and host a great biodiversity in the understory (Mitchell 1992). Oaks are usually grown after clear-cuts, otherwise they are outcompeted by more shade-tolerant species such as beech (Truhlář 1997). Oak monocultures therefore provide habitats that are heterogeneous in light intensity and support light-demanding species (Spiecker 2003). In our study, we found tree diversity to decrease herb diversity, via competition for light (Chapter 4). But the abundance of *Quercus* had a positive effect on herb diversity, mediated through a reduction in the humus mass, indicating that at the scale of the forest, it is important to keep some oak monocultures, in part for conserving understory herb species. More work is needed to construct economical models for forest management, which would include biodiversity and species identity effects on forest functions (Spiecker 2003; Knoke *et al.* 2007; Burger 2009).

Future research

The results presented in this thesis are only a fraction of the possibilities offered by the large dataset compiled, and I intend to pursue this work to broaden the picture. The next obvious angle that I intend to take relates to site productivity and stability. I first will compute climate correlations at the site level, to see if the effective number of species and the density of trees in a stand affect species response to climate. Then I will use allometric equations to upscale diameter growth to biomass accumulation for all the trees that were cored. Hopefully, having a

common scale for all species will allow me to look at the effects of diversity on stand productivity, even though I will need to account for propagating errors in the allometric estimation, in contrast with known DBH with ignorable error. If the allometric estimations prove robust, I will calculate the relative contributions of the selection and complementarity effects with the method from (Loreau & Hector 2001). Sadly since Turnbull *et al.* (2013), we know that we can get positive complementarity effects with scenarios with no coexistence and with included niches, so not the complementarity in the sense that most ecologists intend. However the assumption of included niches is not always realistic, esp biotic interactions. Some long-term experiments show that high diversity mixtures might be stable over time, and species are anyway chosen from a pool of coexisting species, at least at the regional scale. Given the sampling design that was chosen here, this might not be possible because the target trees for which we have annual growth are scattered in each site. Another possibility to expand this work would be to design another experiment in mature forests, where all trees in plots would be cored. This would make it possible to track each tree's neighborhood through time, and explore the effects of diversity and density at each point in time. Besides, all trees being cored in a plot would justify calculations of productivity and stability at the population and community levels.

Conclusion

In this thesis, I show that tree diversity has mostly positive or at least neutral effects on several functions in a managed forest of central Europe. Specifically, I found positive effects of tree diversity on individual tree growth (Chapter 2), and on the species richness of earthworms and saproxylic beetles (Chapter 4). I found tree diversity to have neutral effects on tree climatic response (Chapter 3), stand wood removal (Chapter 1) and on the diversity of detritivorous and predatory beetles (Chapter 4).

The only negative effect of tree diversity was found on herb diversity, due to competition for light (Chapter 4). Therefore, future forest practices should emphasize biodiversity even more than they do today. However, the interacting effects of tree species identity and diversity with those of climate change should be integrated in an economical modeling framework for forest management.

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